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ON A NEW POLYEMBRYONIC ENCYRTID (CHALCIDOIDEA) *COPIDOSOMA TORTRICIS* SP. N. BRED FROM THE STRAWBERRY TORTRIX MOTH.

BY JAMES WATERSTON, B.D., B.Sc.

(Published by permission of the Trustees of the British Museum.)

(With 5 text-figs.)

DURING the course of investigations into the life history of the Strawberry Tortrix (*Oxygrapha comariana* Z.) in 1918 and 1919, of which the results appear elsewhere (p. 6), Mr F. R. Petherbridge reared a small chalcid in numbers and was good enough to send me some of his material for study. With the hymenoptera there were fortunately enclosed two of the irregularly swollen dried skins of the hosts whose remarkable appearance (Fig. 1) at once suggested a polyembryonic method of reproduction on the part of the parasite. Although Mr Petherbridge could supply no direct evidence on this point he had made the significant note that as many as 35 of these parasites might emerge from one larva.

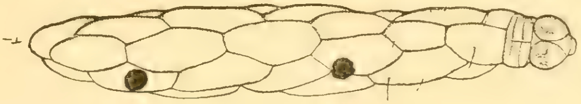

Fig. 1. Larva of *Oxygrapha comariana* Z., showing the characteristic swellings produced by the pupation of *Copidosoma tortricis* Wtrst. with holes of emergence of the parasite.

Having dissected and thoroughly examined both sexes of the chalcid I came to the conclusion that it should be assigned to the genus *Copidosoma* Ratz. but neither the named material in the British Museum collection—at present in an unsatisfactory state—nor a study of Mayr's Monograph of the European Encyrtidae enabled me to determine the species. Recently I have submitted both dried specimens and various preparations of the *Copidosoma* to my friend Prof. F. Silvestri who, however, can suggest no definite name for the insect though he knows it well, having reared a practically identical form from a *Tortrix* sp. in Italy. As Prof. Silvestri tells me he has found this *Copidosoma* to be polyembryonic in Italy I have no doubt the British form is so too.

Superfamily: CHALCIDOIDEA.
Family: ENCYRTIDAE.
Genus: **Copidosoma** Ratzeburg (1844).

Copidosoma tortricis sp. n.

Distinguished by the proportions and chaetotaxy of the antennae (♂, ♀) (Fig. 3 *a*, *b*) especially by the short second funicular joint (♂); the proportions of the head (Fig. 2 *b*); labrum (Fig. 2 *c*); and radius (Fig. 5). The colour of the antennae is probably also of importance.

Note. The proportions of the antennal joints must be studied in properly prepared mounts. In naturally dried specimens there is considerable distortion and the club (♀) in particular is liable to appear unduly flattened. The filamentous end of the preapical dorsal mandibular bristle (Fig. 2 *a*) is often broken off.

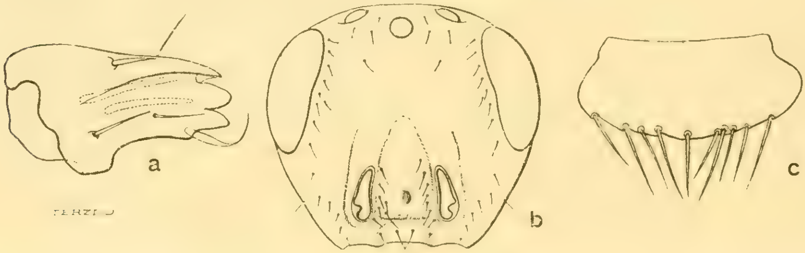

Fig. 2. *Copidosoma tortricis* Wtrst. ♀. (*a*) right mandible from inside, (*b*) head from in front, (*c*) labrum.

A dark blackish brown species in both sexes, with metallic reflections on head and thorax and submetallic on the abdomen dorsally.

♀. Reflections variable but mainly as follows. On face, frons, vertex, pronotum and scutum mainly dark green or aeneous green; on scutellum and mesopleurae (more shining) and abdomen (more dully) purplish. Outer aspect of hind coxa submetallic.

Antennae concolorous, blackish brown. Palpi paler than rest of trophi. Wings sub-hyaline very faintly and uniformly tinted; neuration brownish, indistinctly and shortly clouded at the base of the radius distally. Legs all tarsi paler, fore and hind coxae, trochanters, femora (except the extreme apex), tibiae (except for a narrow basal ring and in the fore pair sometimes the tip obscurely) blackish—the excepted portions paler. In the mid legs the coxa is dark, trochanter, base of tibia (narrowly) and apex (more broadly) paler. The main portion of the mid femur is brown, not nearly so dark as the fore or hind femora. Mid tibiae variable—as pale as the fore tarsus with an indistinct darker dorsal streak.

♂ similar to the ♀ in colour but with definitely darker legs in which the knees, tarsi and sometimes the apex of the fore tibia (obscurely) alone are paler.

♀. Head (Fig. 2 *b*), just broader than long (13 : 12). Eyes rather short and little more than half (5 : 9) the length (depth). Frons very wide, the eyes at the level of the anterior ocellus separated by about ½ and on the base line by ⅞ of the breadth. Malar space large, the malar impressed line ⅘ the depth of the eye or barely half (4 : 9) that of the head. Toruli elongate, much longer (12 : 5) than broad; distant from the clypeal edge at ½, and from one another rather over, their own length. Besides the usual short bristles along the orbits frontally, there are two (1 : 1) minute, below the anterior ocellus, 6–7 on each side between the toruli and 4 (1 : 2 : 1), stronger on the clypeus, remote from the edge. The intertorular area is somewhat tumescent. Pattern moderate, regular, distinctly but not strongly raised.

Antenna (Fig. 3 *b*). Length about 1 mm., scape and bulla together not quite half as long as the remainder of the antenna. Scape (6 : 1) nearly thrice the pedicel (7 : 4) longer than the first four joints of the funicle and about ¼ longer than the club. Funicle expanding from the second joint onwards, sixth joint nearly as wide as the club and much broader (7 : 4) than the first, but only a little longer (9 : 8). The insertion of the funicular joints is infra median and the distal superior angle is indistinctly produced and setigerous. The club is distinctly segmented only on one side and the sensoria are few. Labrum (Fig. 3 *c*), mandibles (Fig. 3 *a*) elongate, tridentate, maxillary palpus 12 : 10 : 15 : 25. Last joint with four stouter bristles (1 median, 2 preapical, and 1 apical) at the edge (of which the last is ⅔ the joint) and 14–16 finer over its surface. Labial palpus 12 : 15 : 12, apical bristle as long as the joint which bears 6–7 in all.

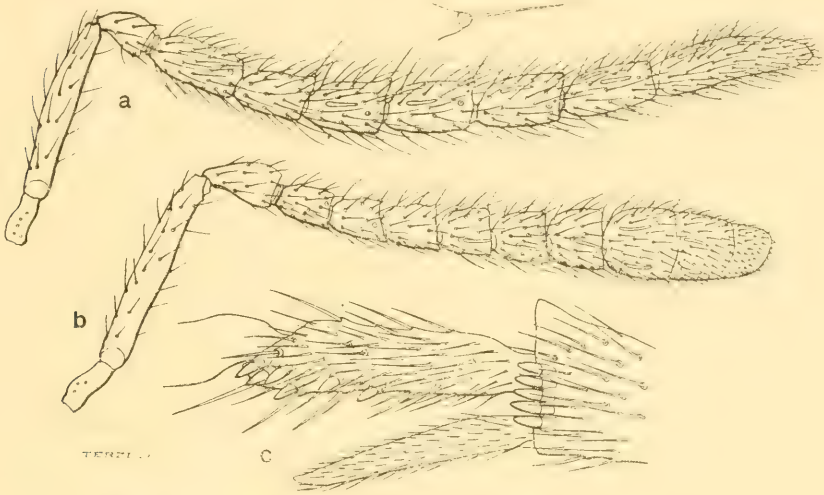

Fig. 3. *Copidosoma tortricis* Wtrst. (*a*) Antenna ♂, (*b*) antenna ♀, (*c*) first joint of mid tarsus and apex of tibia ♀.

Thorax and propodeon subequal, both in length and breadth to the abdomen, but broader than the head. Thorax + propodeon + head shorter than antenna.

Pronotum, posterior row of about 18 bristles. Prosternum twice as broad as long. Prepectus entirely reticulate. Tegulae three bristles. Axillae not quite touching, with one minute bristle. Scutellum, about $\frac{1}{6}$ shorter than the scutum with about 30 bristles. Propodeon extremely short spiracle small, broadly oval, situated at the extreme side where the segment is intumescent and posteriorly angulate. One or two pleural bristles and another small patch of the same behind the spiracle, the individual bristles rising from minute wart-like excrescences.

Wings, forewings (Fig. 4) (7 : 3) length 1·3 mm., on the submarginal vein 12–14 bristles. Radius (Fig. 5) with a single bristle and four terminal pustules, on the dorsal surface along the edge of the submarginal cell are about 30 bristles. Below nearly the whole surface of the cell is covered with bristles of which about 10 towards the apex are longer and oblique. There are 6–8 rows of bristles basally before the "hairless streak." Hind wings (7 : 2) length ·8 mm. Forelegs, femur equal to tibia. The latter with comb of six rather long spines apically. Upper apical angle of tibia with one chitinous tooth anteriorly and another posteriorly, first tarsal comb of 12 spines. Proportions of first three tarsal joints, 9 : 6 : 5.

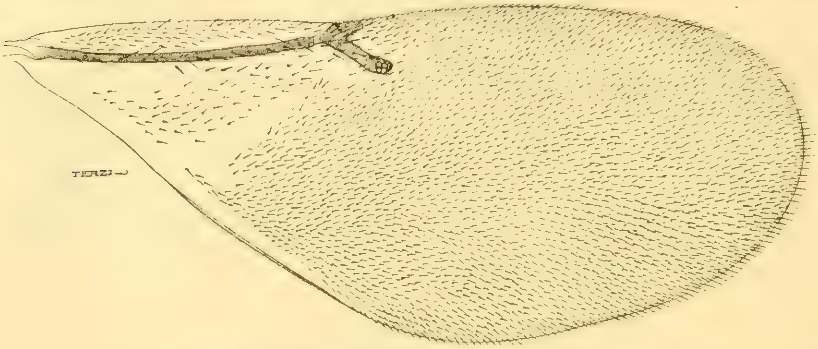

Fig. 4. *Copidosoma tortricis* Wtrst. ♀ wing.

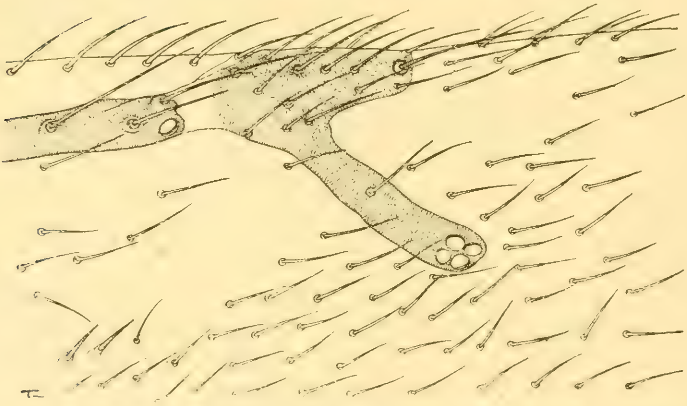

Fig. 5. *Copidosoma tortricis* Wtrst. ♀. Details of radius of wing.

Mid leg, femur shorter (6 : 7) than tibia. Spur of the latter shorter than first tarsal joint (Fig. 3 *c*). Heavy spines on apex of tibia 5, on tarsus 6, 4, 4, 2, 0, respectively. Tarsus, 14 : 7 : 6. Hind legs, femur shorter (5 : 6) than tibia, comb of the latter 10 spines, longer spur $\frac{5}{8}$ of the first tarsal joint, second very short about $\frac{1}{4}$ of the first. Tarsus 12, 8, 7.

Abdomen. Along the mid line the first tergite exceeds all except the seventh, which is slightly longer, 2–4 and 6 are subequal, 5 longer. Setigerous process half as broad again as long, with 3 long and 1 shorter seta. Distance between the processes greater (3 : 2) than the longest seta or (3 : 1) than the distance from either process to the spiracle. The latter minute, circular, 12–14 bristles distally on spiracular overlap. Pattern of abdomen raised and coarser anteriorly on first tergite, smoother posteriorly and medianly. Terebra distinctly shorter than its sheath. Distal portion of the latter ($\frac{5}{6}$ the base) with one bristle. 3–4 bristles apically on the pleural flap above.

Length 1·3 mm.

Alar expanse, 3 mm.

♂. Head, broader than long (nearly 5 : 4) much broader relatively than in ♀. The base line of the eyes cuts off the upper $\frac{1}{4}$ of the toruli. The latter at their nearest separated by more than, and from the clypeal edge by $\frac{6}{7}$ of, their own length.

Antenna (Fig. 3 *a*), length 1·1 mm. Scape over thrice the pedicel equal to the first two and $\frac{1}{3}$ of the third funicular joints together. Funicle of practically equal width but widest on the third joint with the unsegmented club tapered apically. The second joint is the shortest.

Throughout the antenna bears numerous moderately strong fuscous bristles which are more or less curved apically. At the upper distal angle (in profile) of each funicular joint and about the middle of the dorsal edge of the club is a tubercle (very conspicuous on joints 2–4) emitting a single characteristic fine *hyaline* bristle. Being neither coloured nor apically curved, these bristles in spite of their fineness are exceedingly conspicuous. There are few sensoria.

Thorax and propodeon together shorter than abdomen.

Wings. Forewings a little over twice as long as broad, about the same length (1·3 mm.) as in the ♀ but broader. Hind wings slightly more (22 : 7) than three times as long as broad.

Forelegs, tibia just shorter than femur.

Abdomen, tergite 7 longest—half as long again as 1.

Last sternite apically broadly emarginate. Genitalia. Basal plate with 6–7 bristles on each side. Paramer bidentate, rather slender, about $\frac{2}{3}$ the breadth of the plate in length.

Dimensions much as in ♀ the abdomen however slightly longer.

Type ♀ in Brit. Mus. one of a series (♂, ♀) bred from larva of *Oxygrapha* (*Peronea*) *comariana*, Z., England, Cambridge, Summer 1918 and 1919 (F. R. Petherbridge).

(The figures illustrating this paper are reproduced by permission of the Ministry of Agriculture.)

THE LIFE HISTORY OF THE STRAWBERRY TORTRIX, *OXYGRAPHA COMARIANA* (ZELLER).

By F. R. PETHERBRIDGE.

School of Agriculture, Cambridge.

(With 1 Plate.)

The first record of serious damage by the caterpillars of this moth was made by Miss Ormerod[1], from notes sent by Dr Ellis of Liverpool in 1883, who in turn recorded them from Mr Richard A. Wrench, of Dee Banks, Chester. The strawberries attacked were in the neighbourhood of Dee Banks.

The next record is by Theobald[2] who records them as doing serious damage to a field of strawberries belonging to Messrs G. Mount and Sons.

From 1913–1917 they caused serious damage to strawberries at Terrington St Clements, Walpole and Walton between King's Lynn and Wisbech, and in several cases reduced the crop to about 25 per cent. of a normal one, with the result that many acres of strawberries were ploughed up as being unprofitable. In 1918 they were recorded by Theobald as present in Warwickshire, Somerset and Hertfordshire.

Life History. The young larvae begin to hatch out at the end of April or early in May. In 1918 they were found on April 21st, but in 1917 and 1919 they were not found until the first week in May. As soon as they hatch they begin to feed on the very young folded fan-shaped leaves and to make holes through the successive layers: sometimes they leave the upper epidermis intact. They remain sheltered by the folded leaves so that they are not visible until the leaves are unfolded. After a time some of the larvae begin to feed on the unopened flowers. They bore a hole through the folded calyx and feed on the stamens and developing carpels, with the result that the flowers attacked either do not form fruit or form only distorted ones.

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[1] Ormerod, E. A. *Handbook of Insects Injurious to Orchard and Bush Fruits*, pp. 258–260.

[2] *The Journal of the South-Eastern Agricultural College*, 1911.

The caterpillars bind the leaflets, and often several leaves together, by means of threads, this providing an easy means of recognising an attack. They also make little webs on the backs of leaflets under which they feed and moult. They can crawl fairly quickly, and when touched they wriggle in the characteristic tortrix manner. Sometimes they suspend themselves from the plants by means of long threads.

The caterpillars hatch over a fairly long period and remain feeding until nearly the end of June (June 29th in 1916; June 15th in 1917; June 25th in 1918).

Pupation takes place in the webs on the leaves which have been spun together, i.e. where the larvae have been feeding. It usually starts early in June, but may take place at the end of May (May 23rd, 1911, Theobald; June 1st, 1917; June 11th, 1918).

The moths begin to hatch out in June (June 7th, 1911, Theobald; June 21st, 1917) and may be found up to the end of July. They may be found sitting on the leaves or crawling about in the centre of the plants, and may often be seen to fly short distances when disturbed. Apparently they are not capable of flying far, as the attack has spread very slowly. Fields adjoining others badly attacked remained free from attack for two years. This first brood of moths lay their eggs during July usually on the backs of the stipules at the base of the plant, but occasionally on the lower part of the leaf stalks. Moths brought from Walton on July 11th, 1917 were put on strawberry plants in a breeding cage. Young caterpillars were first found on July 21st. Caterpillars were found at Walton on July 18th and also at intervals until September 5th.

Pupae were found on August 19th, 1917 and until September 20th. Moths were found on September 11th and were present until November 17th. After this date no moths were found until the following June. Several observers suggest that the moth hibernates. Theobald says[1] "The moths apparently hibernate, for I have taken them by beating in late October at Buxton and again in the early spring at Wye."

Although I searched carefully for these moths during the winter and spring I found none from December to June, and I came to the conclusion that the moths do not hibernate. Moreover a large number of eggs were present on the plants from November onwards. This has an important practical bearing, for by ploughing up a piece of strawberries in December, the eggs will almost certainly be prevented from giving rise to moths next spring.

In 1917 a few eggs were first found on the stipules on November 3rd and they gradually increased in number until the middle of the month. Most of the eggs in 1917 were laid during the first half of November, as during that time numbers of eggs were laid in the boxes in which the moths were brought from Walton. In 1918 eggs were found on October 25th, but owing to the scarcity of moths due to the killing of the larvae by Chalcid parasites, it was difficult to tell how long the moths lived. None were found after the middle of November.

---

[1] Theobald, *Insect Pests of Fruit*.

Two moths were found about two feet from the ground on some sticky bands on apple trees near which some strawberry plants had been heeled in.

The following table shows the life history of the pest in 1917. This seems to be a fairly normal one, but there are seasonal variations as mentioned above.

Stage	When found	Length of life of the various stages
Caterpillar	Beginning of May—middle of June	4–5 weeks
Pupa	During June	2–3 ,,
Moth	Last week in June—end of July	4 ,,
Egg	Last three weeks of July	1 week
Caterpillar	Mid July—beginning of September	4–5 weeks
Pupa	Third week in August—end of third week in September	2–3 ,,
Moth	Second week in September—third week in November	about 8 ,,
Egg	Beginning of November—middle of May	about 6 months

The eggs are laid singly usually on the outside of the stipules, but occasionally on the lower part of the petioles. Two or three eggs may be present on one stipule.

The egg is very flattened, and broadly oval in outline, measuring 0·86–0·96 mm. in length and 0·64–0·69 mm. in breadth. The shell of the egg is of a silvery white colour, beautifully sculptured, being covered all over with a raised network which is best seen round the edges while the developing larva is still present (Pl. I, fig. 1). The developing larva is at first yellowish, but later assumes a reddish orange colour. The egg is easily seen owing to the whitish rim of the shell which extends beyond the developing larva.

The larva varies according to its stage of development, so much so, that at first I thought I was dealing with two different species.

In the young larval stages the head and the first thoracic plate are shining black, but in the older stages they are yellowish.

I watched a larva about 6 mm. long, with a black head and thoracic plate, in the process of moulting, and found that the head and thoracic plate of the remaining larval stages remained yellow.

On hatching it measures 1·9–2·1 mm. and when full grown 9·5–11 mm. in length. In the young larval stages the body is of a dirty white or dirty yellow colour and the short legs are brownish black, except at their bases, which are greenish. The head and body are hairy as in the later stages (see Pl. I, fig. 2).

In the older stages the head is yellowish, semi-transparent, with light brown splashes on the vertex, and with a pair of black spots on each side, which are not visible when the caterpillar is looked at from above. The anterior of these spots is situated just behind and below the antenna and round the group of eyes. The posterior one is situated at the same level near the posterior margin (see Pl. I, fig. 2).

The first thoracic plate is of a pale yellowish colour in those larvae which have a yellowish head. These later stage larvae have legs of a yellowish brown colour.

The body is at first of a dirty white or dirty yellow colour, but later on may be either a dull yellowish green, a yellowish brown or a dull green colour.

The dorsal vessels appear as a dark green line down the middle of the body and can be seen pulsating. On each side of it is a sub-dorsal line of a dark colour.

The pupa is 6·5–7·5 mm. in length and very variable in colour. At first the head is brown, the wing cases green and the abdomen brownish yellow; but later on the green colour usually disappears and the wing cases become yellowish brown and the abdomen reddish brown.

The moths are also very variable in colour. The triangular patch on the fore wing may be of a rich brown colour or almost black.

Parasitism. In 1918 both broods of caterpillars were badly parasitised by the larvae of a small Chalcid[1]. As many as 35 Chalcids were reared from a single caterpillar. The larvae eat the inside of the caterpillar and leave only the skin. The outline of each larva can be seen through the transparent skin. They cause the skin to bulge. The first brood of adult chalcids appears in July, and although I found chalcid pupae in October I have no record of the date of appearance of the second brood of adults. A single pupa was found containing a large hymenopterous parasite, but this did not mature.

Remedial measures.

In 1918 I tried the effect of spraying attacked plants with Lead Arsenate and with powders containing Calcium Arsenate and Calcium

---

[1] A description of the parasite is published on p. 2 of this number of the *Journal.*

Arsenite respectively. These sprays did not succeed in reducing the caterpillars to any extent, probably due to mechanical difficulty of reaching with the spray the young folded leaves on which the young caterpillars feed.

Many of the growers who sprayed with Lead Arsenate were pleased with the results, but they were then probably not aware that, thanks to the energies of the chalcid parasites, the caterpillars had almost disappeared from strawberries which were not sprayed.

Apart from parasites, the best means of reducing this pest seems to be to run a mowing machine over the crop so as to cut off the tops as close to the crown as possible when the pest is in the second pupal stage, viz. at the beginning of September. (It is a common practice with many growers to cut off the tops during the autumn.) The tops must then be raked up and burnt or buried before the moths come out, i.e. the middle of September. I tried this on one field but unfortunately the grower waited too long before destroying the tops. (NOTE: the eggs are laid too low down to be cut off in this manner.)

Old strawberry beds destined to be ploughed up should be ploughed after the eggs are laid in November, as by ploughing earlier than this the moths will probably lay their eggs on neighbouring crops of strawberries, or on wild plants of Fragaria and Comarum near.

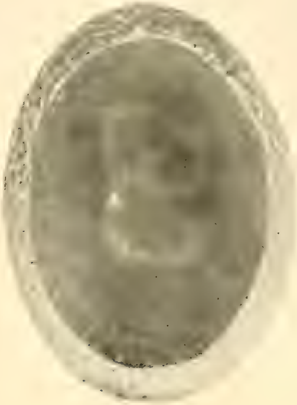


Fig. 1. The egg of *Oxygrapha comariana* (× 56).

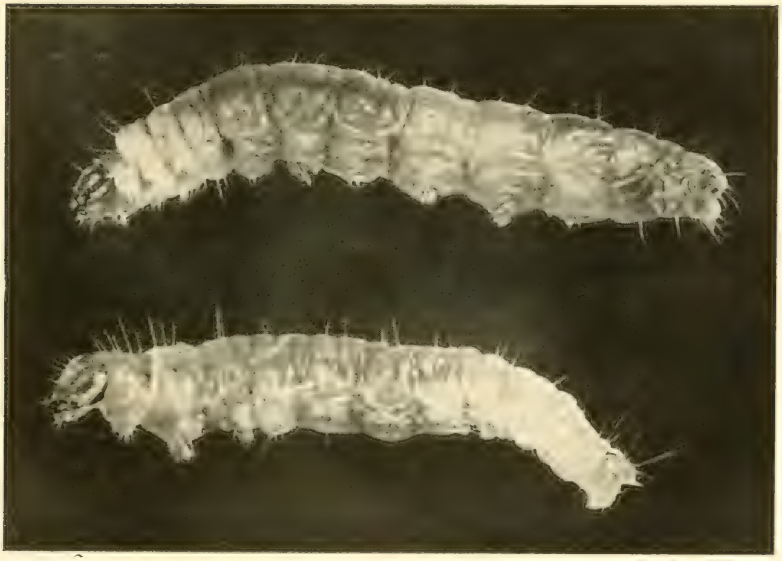


Fig. 2. Late stage larvae of *Oxygrapha comariana*.

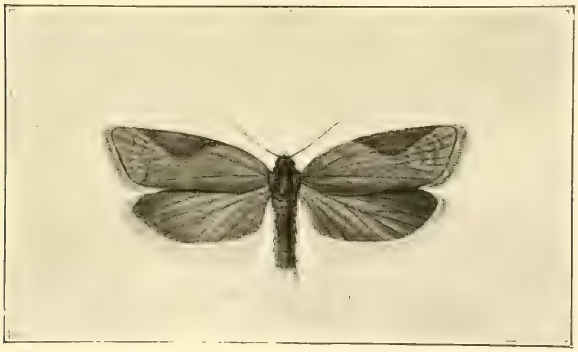


Fig. 3. *Oxygrapha comariana* (after Theobald).

DAILY PERIODICITY IN THE NUMBERS OF ACTIVE SOIL FLAGELLATES: WITH A BRIEF NOTE ON THE RELATION OF TROPHIC AMOEBAE AND BACTERIAL NUMBERS.

By D. WARD CUTLER and L. M. CRUMP.
(*Rothamsted Experimental Station.*)

(1 Map and 7 text-figs.)

In a recent paper by one of us (4) are given the results of periodical counts of the protozoa found in certain of the Rothamsted fields. These numbers refer, however, to the total protozoan population irrespective of their physiological conditions—cystic or trophic. A method (6) has recently been devised by which these two states can be separated and the numbers counted. From October 8th, 1919 to January 29th, 1920 fortnightly soil samples were taken from the dunged plot of Rothamsted wheat field and the trophic and cystic protozoa counted.

Fig. 1 gives the active numbers per gr. of soil for three species of flagellates (*Oicomonas* sp. (Martin), *Cercomonas longicauda*, Bodo sp.), the numbers of trophic amoebae and the bacterial numbers. On the same curve is also given the moisture content of the soil. Fig. 2 shows the curves for the daily rainfall and soil temperature 1 ft. depth (Meteorological Office type thermometer) during the period.

Examination of these curves suggests no correlation between the number of active organisms and the temperature or water content, but there is an indication of periodicity in the fluctuations of numbers of active flagellates. The sudden rise in numbers on Nov. 13th is probably due to addition of manure to the soil seven days previously. It is interesting to note, however, that this did not prevent cyst formation and subsequent reduction in active numbers on Nov. 25th.

As the soil samples were taken at approximately fortnightly intervals the figures give no information as to the daily fluctuations in number of the protozoa—obviously a matter of great interest; to determine this daily samples were taken from the Broadbalk dunged plot—the first on Feb. 9th, 1920.

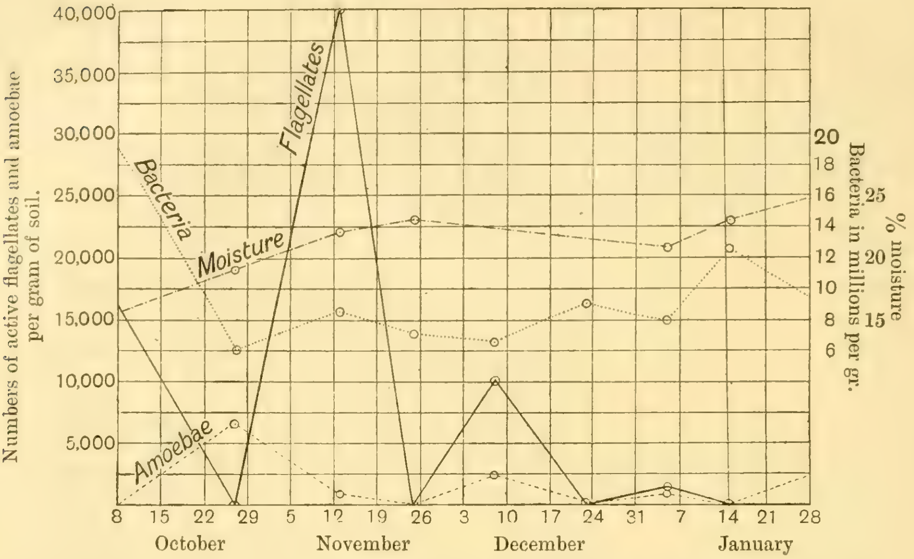


Fig. 1. Numbers of active flagellates, amoebae and bacteria per gramme of soil and percentage of moisture in Broadbalk, plot 2, from October 8, 1919—January 28, 1920. Bi-monthly countings.

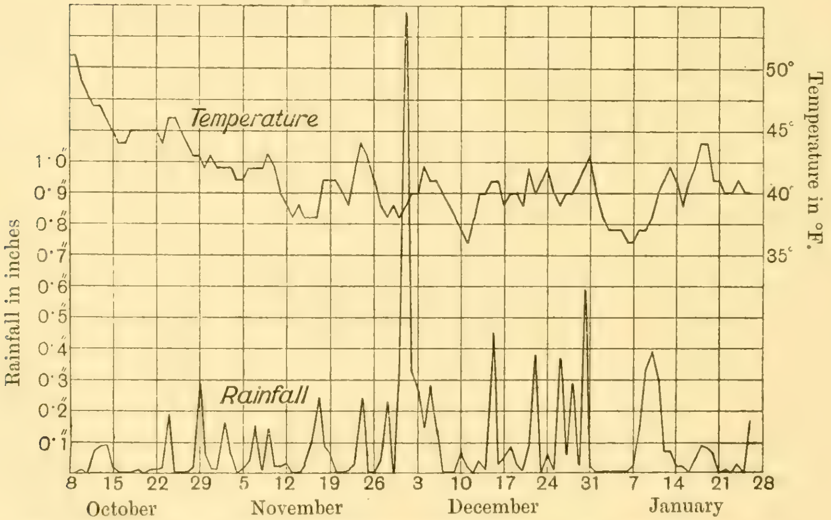
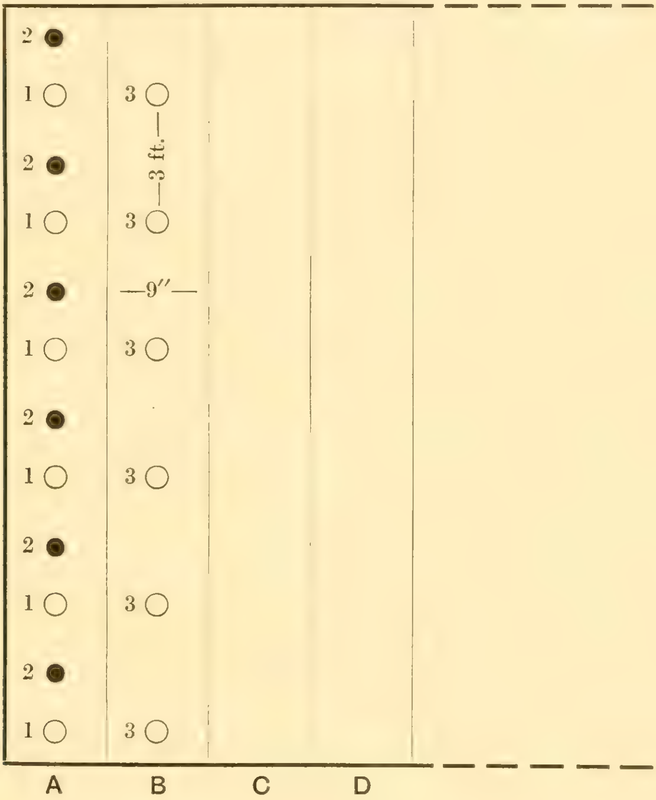


Fig. 2. Rainfall and ground temperature from October 8, 1919—January 28, 1920.

METHODS.

The method of sampling was as follows: In the centre of the plot 14 rows between the young wheat plants were selected. Four of these—A, B, C, D—are shown in the accompanying map.

Six 9-inch borings, taken at intervals of about 3 ft. along row A, and thoroughly mixed together formed sample 1, which was taken to the laboratory in a sterile bottle.



Map showing method of taking samples.

The second sample was taken the following day in the same way as the first, except that the borings were taken between those of the previous day.

The samples for the third and fourth days were taken in the same manner as the sample for the first and second, but from row B. In this way 28 samples were obtained from 14 rows of the plot. The counting method employed is a dilution one, fully described in a recent paper(6). Briefly, it consists of dividing the sample into two 10 gr. portions. One of these is made up into a series of suitable dilutions, from each of which 1 c.c. is inoculated on to agar plates which are incubated at 18° C., and examined at 7 and 14 day intervals. If, for example, growth occurs in the 1/1000 dilution plates there was at least one organism producing this growth, and it is assumed that there are at least 1000 per gr. of soil. Thus by using dilutions sufficiently near to one another the total number of protozoa per gr. of soil can be ascertained. To find the number of active forms the second 10 gr. portion of the soil is treated overnight with 2 per cent. HCl; this kills all active forms leaving the cysts uninjured. The number of protozoa in this treated sample subtracted from that in the untreated gives the number of active protozoa per gr. of soil. Proof of the accuracy of this method is given in the paper referred to above, and further proofs are annexed on pp. 14 and 16 of the present paper.

RESULTS OF DAILY COUNTS.

The daily numbers of active and cystic forms of the three species of flagellates are given in Table I and Figs. 3 and 4. It will be seen that the total numbers—trophic and cystic—exhibit great fluctuations, rarely being the same for two days together. The most remarkable feature presented by the results, however, is the wholly unexpected daily periodicity in the fluctuation in numbers of the trophic forms. We think there is no doubt as to the reality of this periodicity.

Table I. *Giving the total—cystic and active—numbers per gr. of soil for three species of flagellates on successive days, beginning February 9th and ending March 8th*, 1920.

Day	Total	Cystic	Active	Day	Total	Cystic	Active
1	9,000	5,000	4,000	15	15,000	3,250	11,750
2	6,000	6,000	0	16	15,000	6,500	8,500
3	9,000	3,250	5,750	17	15,000	3,000	12,000
4	2,500	1,800	700	18	6,500	6,500	0
5	6,500	2,500	4,000	19	20,000	1,000	19,000
6	5,000	5,000	0	20	7,500	3,250	4,250
7	9,000	600	8,400	21	9,000	2,500	6,500
8	5,000	2,500	2,500	22	6,500	2,500	4,000
9	5,000	1,000	4,000	23	15,000	3,250	11,750
10	1,500	1,000	500	24	5,000	3,250	1,750
11	9,000	1,000	8,000	25	10,000	1,500	8,500
12	6,500	3,250	3,250	26	5,000	2,500	2,500
13	15,000	1,000	14,000	27	6,500	1,000	5,500
14	10,000	6,500	3,500	28	25,000	25,000	0

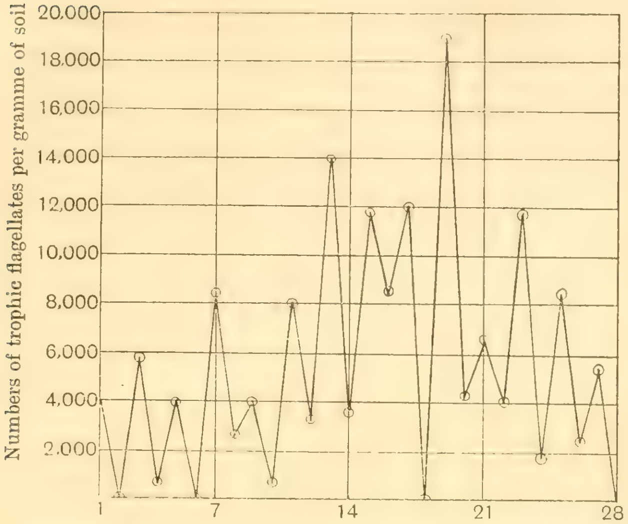


Fig. 3. Active flagellates in Broadbalk, plot 2, from February 9—March 8, 1920. Daily countings.

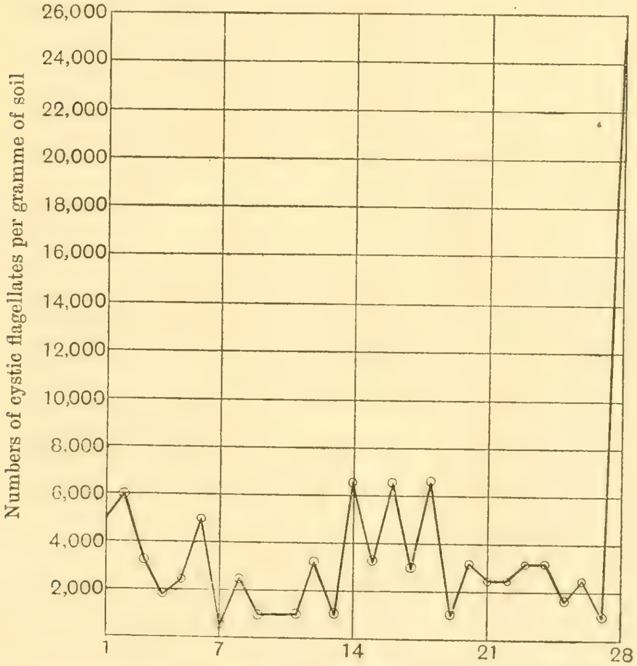


Fig. 4. Cystic flagellates in Broadbalk, plot 2, from February 9—March 8, 1920. Daily countings.

The regularity of the alternation is evidence of the reliability of our methods; for it is almost impossible to believe in an experimental error having so constant and so distinct a rhythm.

The possible sources of error are:

1. Method of counting.
2. Uneven distribution of protozoa in the field.
3. The death of cysts as well as of active protozoa by the use of 2 per cent. HCl.

Method of Counting. The paper in which this method is described (6) gives proof of its accuracy; a few further examples may, however, be given.

Table II.

	Amoebae		Flagellates		Ciliates	
	Active	Cystic	Active	Cystic	Active	Cystic
1. Number organisms added	40,000	25,000	100,000	100,000	5,000	32,500
,, ,, after treatment		25,000		95,000		30,000
2. Number organisms added	50,250	96,800	130,000	560,000	35,000	10,000
,, ,, after treatment		95,000		500,000		10,000
3. Number organisms added	20,000	15,000	90,000	45,000	35,000	15,250
,, ,, after treatment		12,500		40,000		10,000
4. Number organisms added	4,000	2,500	6,500	1,500	5,000	25,400
,, ,, after treatment		2,000		1,000		20,000
5. Number organisms added	537,000	645,000	1,500	1,000		
,, ,, after treatment		600,000		900		
6. Number organisms added	30,000	50,000	250,000	100,000	2,500	5,000
,, ,, after treatment		45,000		85,000		4,000
7. Number organisms added	50,250	40,000	50,000	250,000		
,, ,, after treatment		35,000		200,000		
8. Number organisms added	10,000	5,000	20,000	2,500		
,, ,, after treatment		4,500		2,000		
9. Number organisms added	12,500	35,000	15,000	100,000	25,000	1,000
,, ,, after treatment		32,500		85,000		1,000
0. Number organisms added	150,000	10,000	250,000	200,000		
,, ,, after treatment		9,000		150,000		
11. Number organisms added	20,500	30,000	15,250	32,500	5,000	10,000
,, ,, after treatment		25,000		26,500		8,000
12. Number organisms added	250,000	15,000	25,000	2,500	2,500	2,500
,, ,, after treatment		12,500		2,000		2,000
13. Number organisms added	100,000	250,000	250,000	35,000		
,, ,, after treatment		250,000		30,000		
14. Number organisms added	1,500	95,000	40,000	5,250	5,000	20,000
,, ,, after treatment		80,000		4,500		15,250
15. Number organisms added	50,250	32,500	6,500	96,800	30,000	25,000
,, ,, after treatment		28,000		90,000		20,000

Soil, which had been sterilised in the autoclave under 15 lbs. pressure for half-an-hour, was inoculated with a counted suspension of trophic and cystic protozoa. It was then treated with 2 per cent. HCl. overnight, and the numbers counted by the dilution method. Fifteen such experiments were performed, given in Table II. On five other occasions two samples have been taken near to each other from the same field, and the number of protozoa in each sample found independently by two observers. The results so obtained were in every case identical.

Uneven distribution over the field. This possible source of error appears to us to have been obviated by the method of sampling we adopted. Reference to the map on p. 13 will show that if uneven distribution over the field is to account for the periodicity one must assume that active and cystic flagellates occupy alternate situations over the 14 rows which we sampled. Surely an impossible assumption!

The following experiments, however, will afford proof that the protozoa are fairly evenly distributed. In 1916–17 one of us took soil samples indiscriminately over the plot. These samples were counted and the results are given below.

	Sample	Amoebae	Flagellates
Feb. 16, 1916	1	2,500	50,000
	2	2,500	50,000
	3	2,500	50,000
May 30, 1917	1	3,750	17,500
	2	3,750	17,500
	3	3,750	17,500
	4	3,750	17,500

On March 9th, 1920 (two days after the daily sampling had ceased) two further samples were taken, B and C, and counted independently. The numbers were as follows:

	Total		Active		Cystic	
	Flagellates	Amoebae	Flagellates	Amoebae	Flagellates	Amoebae
Series B ...	9,000	2,500	6,500	2,150	2,500	350
,, C ...	9,000	3,250	5,750	2,650	3,250	600

These figures justify the belief that unequal distribution in the field cannot account for the flagellate periodicity.

Death of cysts due to action of 2 per cent. HCl. In the previous publications referred to above (5, 6) it was shown that a small proportion of the cysts might be killed by the acid; the proportion, however, was on the average below 15 per cent., which could not account for the marked differences obtained in the present series of experiments.

In each case the residual acid was determined by titration and found to be approximately constant, and as there had been so little variation in the conditions of working there is no reason to expect any variation in the action on the cysts. Samples 2, 5, 12, 18, 22 in Table I furnish examples. Here the total number of flagellates are nearly identical: the titration values for the samples are the same, but the number of active flagellates are very different. This also occurs with samples 13, 15, 16, 17.

DISCUSSION.

Table I and Fig. 3 clearly demonstrate a daily periodicity in the numbers of active forms of the three species of flagellates counted in our experiments. The rhythm is not obviously dependent on temperature or rainfall; for the curves of Fig. 7 show no relationship to the number of flagellates. Nor can we find evidence that any other external factor is the cause.

Preliminary experiments in laboratory cultures of the organisms maintained at a constant temperature of 20° C. indicate a similar periodicity. Further work on the subject is now in hand, and any detailed discussion of the causes of these daily fluctuations would be premature until more exact knowledge is gained of the life histories of the flagellates and the time required for the completion of each phase. Further, two of the flagellates—*Oicomonas* and *Cercomonas*—have two methods of reproduction—an asexual one by binary fission and a sexual one, where conjugation leads to cyst production (11), but little is known of the relationship between these two types of reproduction and the period of time occupied by each.

It seems safe to suppose, however, that the periodicity is a reproductive phenomenon. All through the animal kingdom, from the highest to the lowest class, breeding is a periodic phase, not only of the individual, but also of the species. In the protozoa the malaria parasite affords a good example. As is well known the attacks of fever coincide with the breaking up of the rosette phase of the parasite into merozites. Hence in the tertian ague, caused by *Plasmodium vivax*, fever returns every third day, and in quartian ague of *P. malariae*, every fourth day. Thus in these two species of Plasmodium there is a reproductive periodicity which may be kept up for months. A reproductive rhythm has been suggested in other species of protozoa by Calkins (3) for the fission rate of Paramecium, Woodruff (12) and Gregory (8) for this, and other ciliates, and by Boeck (1) for the encystment of Giardia. In the other phyla of the invertebrate kingdom periodicity obtains as in the egg-laying of *Convoluta* described by Keeble (9). There is also the remarkable case of the Atlantic Palolo worm (*Eunice fucata*), which comes out of its hole to liberate the genital segments before dawn on the last quarter of the moon between June 20th and July 25th. H. G. Mayer states that neither the light nor the tide of the last quarter are necessary.

Further, Bohn in 1904 (2) records that sea shore snails taken far from the natural habitat maintain a rhythm synchronous with the tides for a considerable period.

Each group of the vertebrate kingdom affords examples of the same phenomenon, of which advantage is taken by breeders of mammals; for throughout the whole groups not only the individual, but also the species come "on heat" at periods very nearly identical. That this may be caused by external conditions is probable in certain classes, such as the *Amphibia* and *Reptilia*, but in the majority of cases such a connection has not been shown and "internal changes of the organisms" are now generally assumed. An excellent discussion of these phenomena is given in Marshall's book *The physiology of reproduction*.

Periodicity occurs so widely in all living things that by many people it is regarded as one of the characteristics of living matter. McClendon (10) in discussing the chemistry of vital phenomena says "One striking characteristic of the behaviour of organisms and parts of organisms is their periodicity. The human body shows a periodicity that is perhaps most strikingly demonstrated in fluctuations in temperature, being coldest some time near 3 a.m. and warmest about 10 a.m. Each organ has its characteristic periodicity—respiratory centre 16 and heart 72 per minute, and the motor ganglia 50 per second....This rhythm must be due therefore to metabolic changes."

These few examples are sufficient to demonstrate that the periodicity of soil flagellates though so striking, should not be regarded with surprise, but rather as a further example of a wide biological principle.

NUMBERS OF ACTIVE PROTOZOA IN RELATION TO BACTERIAL NUMBERS.

We have reserved to the last the question of the relationship between bacterial numbers and those of active protozoa. Reference to Figs. 1, 3, 5 show that it is impossible to establish any correlation between the bacteria and the number of active flagellates; for while these vary rhythmically from day to day the bacteria show no such orderly fluctuations.

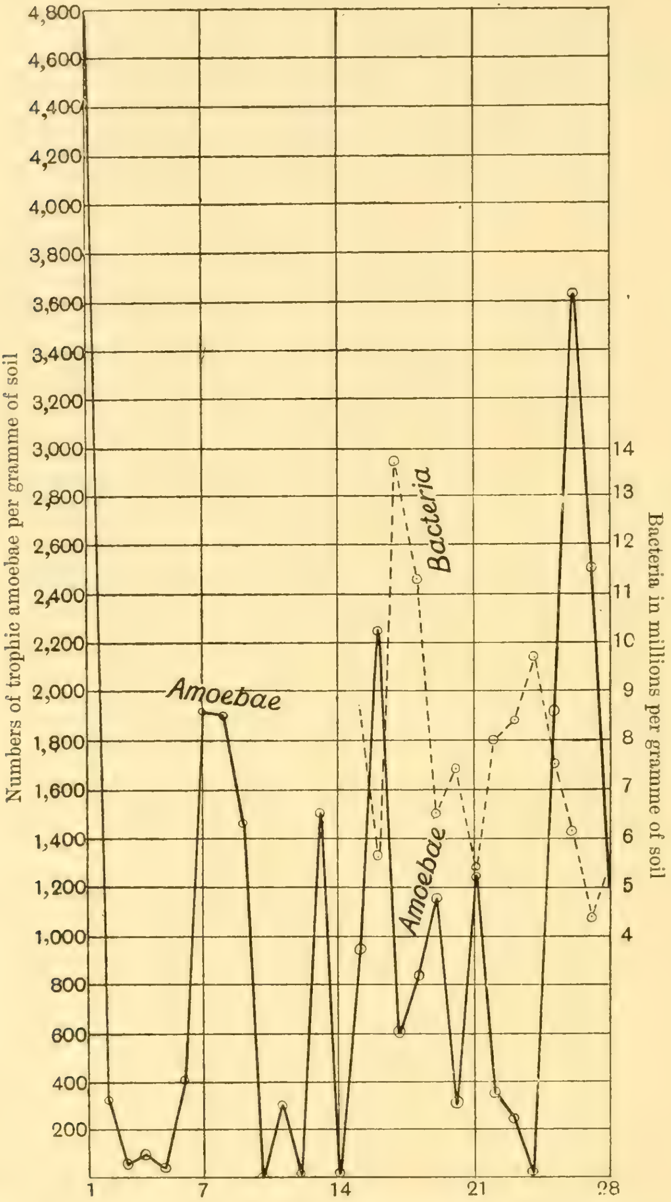


Fig. 5. Numbers of bacteria and trophic amoebae in Broadbalk, plot 2, from February 9—March 8, 1920. Daily countings.

Table III gives the number of bacteria per gr. of soil for 14 daily samples.

Table III.

Sample	Bacteria in millions per gr.	Sample	Bacteria in millions per gr.
15	8·75	22	8·0
16	5·575	23	8·375
17	13·75	24	9·75
18	11·325	25	7·5
19	6·5	26	6·15
20	7·4	27	4·425
21	5·4	28	5·4

The case is different, however, when the trophic amoebae are considered, the numbers of which are given in Table IV. Fig. 5 shows the bacterial and amoebic numbers in 14 daily samples. It is at once evident that there is a very close correlation between the two: without exception when the bacterial numbers are high those of the amoebae are low, and *vice versa*. Russell and Hutchinson postulated such a relationship in their partial sterilisation hypothesis, but we believe this is the first time it has been so clearly demonstrated[1]. By inoculating soil with *Amoeba limax* Goodey (7) was able to bring about a depression in bacterial numbers; but as far as we know data for a curve from ordinary field soil such as Fig. 5 has never before been obtained. This is primarily due to lack of methods. The earlier workers counted the total numbers of amoebae (trophic and cystic); this as was to be expected, gave variable results, and the method ought to be abandoned in future investigations. The second source of error was the length of time between the taking of the samples: they should be taken at frequent intervals, daily if possible. For example, examination of Fig. 5 shows that if after taking sample 17 an interval of three days had elapsed before another was taken both the bacterial and the amoebic numbers would have gone down, and a false conception of the relationship of the two would have resulted. A similar error would have resulted had no counts been taken between samples 19 and 25.

Table IV gives the total, active and cystic numbers per gr. of soil for the amoebae.

Fig. 1 appears to negative the contention of the necessity of daily sampling, for, with one exception the bacterial and amoebic curves fit

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[1] Previous work by one of us showed that the experimental error by our mode of counting bacteria was 17 per cent. This, in the present experiments, would not vitiate the conclusion that there is interaction between amoebae and bacteria.

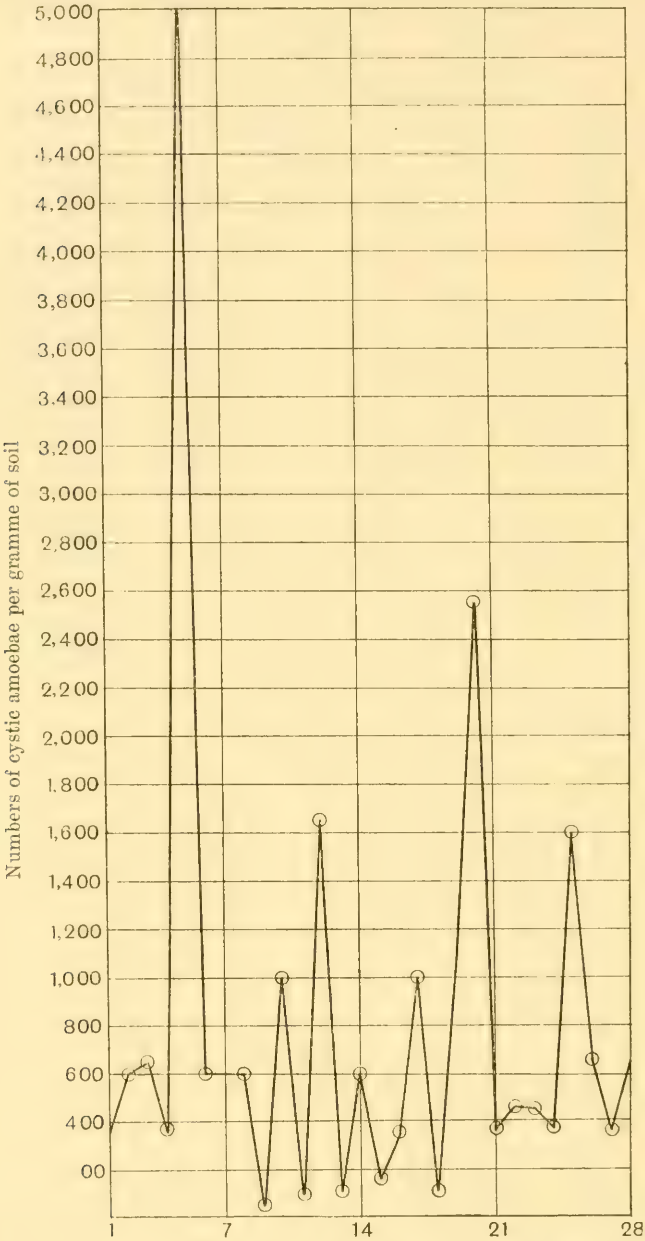

Fig. 6. Cystic amoebae in Broadbalk, plot 2, from February 9—March 8, 1920. Daily countings.

together quite well. This would often occur, but in many cases the correlation will break down if the intervals are long between the successive counts. Doubtless many of the numerous contradictory results in the earlier literature can be ascribed to this cause.

Table IV.

Sample	Total	Cystic	Active	Sample	Total	Cystic	Active
1	5,150	360	4,790	15	1,105	160	945
2	950	610	340	16	2,605	350	2,255
3	705	650	55	17	1,605	1,005	600
4	445	360	95	18	950	110	840
5	5,075	5,030	45	19	2,250	1,100	1,150
6	1,015	610	405	20	2,850	2,550	300
7	2,520	600	1,920	21	1,600	360	1,240
8	2,515	605	1,910	22	810	460	350
9	1,515	55	1,460	23	705	450	255
10	1,010	1,010	0	24	400	375	25
11	400	100	300	25	3,510	1,600	1,910
12	1,660	1,655	5	26	4,275	650	3,625
13	1,610	110	1,500	27	2,855	360	2,495
14	610	600	10	28	1,850	650	1,200

It would be premature to discuss the relation between the numbers of active and cystic amoebae, or the reason why, after a period of depression, the total number of amoebae should suddenly greatly increase.

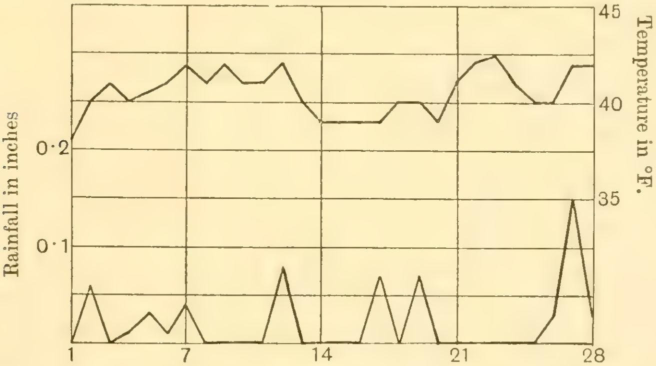

Fig. 7. Rainfall and ground temperature from February 9—March 8, 1920.

The answers to such questions are to be found in a knowledge of the life histories and physiology of these protozoa, which at present we do not possess.

It is hoped to continue the daily counts for a year to obtain data, which, with those yielded by pure culture study, may throw light on the principles underlying the daily fluctuations.

SUMMARY.

1. There is a daily fluctuation in the number of trophic forms of the three species of flagellates *Oicomonas* sp. (Martin), *Cercomonas longicauda* and Bodo sp., in the soil of arable fields.

2. The numbers of bacteria and trophic amoebae in the soil are correlated, varying inversely over a period of 14 days.

3. Temperature and rainfall appear to have no influence on the numbers of active protozoa in the soil.

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SPARTINA PROBLEMS.

By Prof. F. W. OLIVER, F.R.S.

(With 1 Plate and 3 text-figs.)

From time to time the attention, not merely of botanists, but of whole communities is rivetted by the sudden appearance of some unfamiliar plant which spreads everywhere in pure stands, often over great areas and to the almost entire exclusion of other forms of vegetation.

Familiar is the appearance of the fire weed or willow herb (*Epilobium angustifolium*) where forests have been burnt, charlock and field poppy where ground has been broken by the plough or, as in the devastated areas of France, by high explosive shells[1]. In such cases the character of the ground has been modified so as to favour the production of a new type of vegetation, a vegetation which springs suddenly perhaps from dormant seeds long present in the soil.

In other cases a like result is produced by the arrival and spread of some exotic plant gifted with great powers of dispersal such as the Russian thistle (*Salsola kali*) in N. America, and the prickly or pest pear (*Opuntia inermis*) in Queensland and New South Wales[2].

Where fresh water is at once the agent of dispersal and the medium in which the plant grows, very striking effects are apt to be produced—illustrated in recent years by the spread of the water hyacinth (*Eichhornia crassipes*) in the navigable waters of N. America (Florida) and Australia[3], and of Azolla in drains, lagoons and ponds in England and France. More than two generations ago (1842) the newly introduced Canadian waterweed (*Elodea canadensis*) spread with astonishing rapidity through the river and canal systems of England to the material hindrance of navigation and drainage. In this case propagation was certainly vegetative as Elodea is dioecious and female plants alone have been met with in this country. From Britain, Elodea made its way to the

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[1] A. W. Hill, *Kew Bull. Misc. Inf.*, 1917, p. 297.

[2] The Prickly Pear in Australia, Com. of Australia, Inst. of Science and Industry, *Bull.* No. 12, 1919.

[3] H. J. Webber, The Water Hyacinth, *U.S. Dept. of Agric.*, Division of Botany, *Bull.* No. 18, 1897. Water Hyacinth in New South Wales, *Agr. Gaz. of N.S.W.*, Dec. 1906.

Continent where it spread for decades in ever widening circles till it lost itself in the waterless barriers of the Middle East.

The subject of the present article is *Spartina Townsendii*, a reed-like grass which is rapidly monopolising the extensive tidal mud flats of the south coast of England from Dorset to Sussex, with headquarters at Southampton and Poole Harbour. In addition to being a botanical phenomenon of the first order, perhaps unique in the recorded history of vegetation, the spread of Spartina is raising economic problems which will have to be grappled with sooner or later. Though still in the phase of youth Spartina already occupies dozens of square miles of mud flats in pure stands which continually get denser and denser. There seems little risk of error in asserting that in the future this area will expand to hundreds or thousands of miles. Subject to climatic limitations, wherever there is mud there will be Spartina. It is time for us to learn something about the properties of this amazing plant.

A century ago the only species of Spartina known in Europe was *S. stricta*, a low-growing species common on mud flats from Devon to Lincoln and on the Continent. In 1829 this was joined by a second species, *S. alterniflora*, supposed to have been introduced accidentally by shipping from America. Its occurrence in Southampton Water and at one other spot, the mouth of the River Adour, at the southern end of the Bay of Biscay, was well known to botanical geographers in the middle of last century[1]. In 1870 a third species, *S. Townsendii*, the subject of this article, made its appearance in Southampton Water, and it is the spread of this form in recent years which has attracted general attention. Gradually it has made its way east and west from Southampton along the sheltered coast line behind the Isle of Wight. It occurs in special abundance at the Beaulieu and Lymington Rivers and off Keyhaven, behind the Hurst Castle spit. In 1899 the first specimen was discovered in Poole Harbour[2] and in 20 years it has spread into all the inlets and bays in the most remarkable manner[3]. From Poole Harbour no specimens of either *S. stricta* or *S. alterniflora* have been reported.

Into Christchurch Harbour, midway between Poole and Hurst Castle, it penetrated in 1913 and has now established itself in sufficient strength to continue the invasion in force[1]. To the East, whilst Portsmouth,

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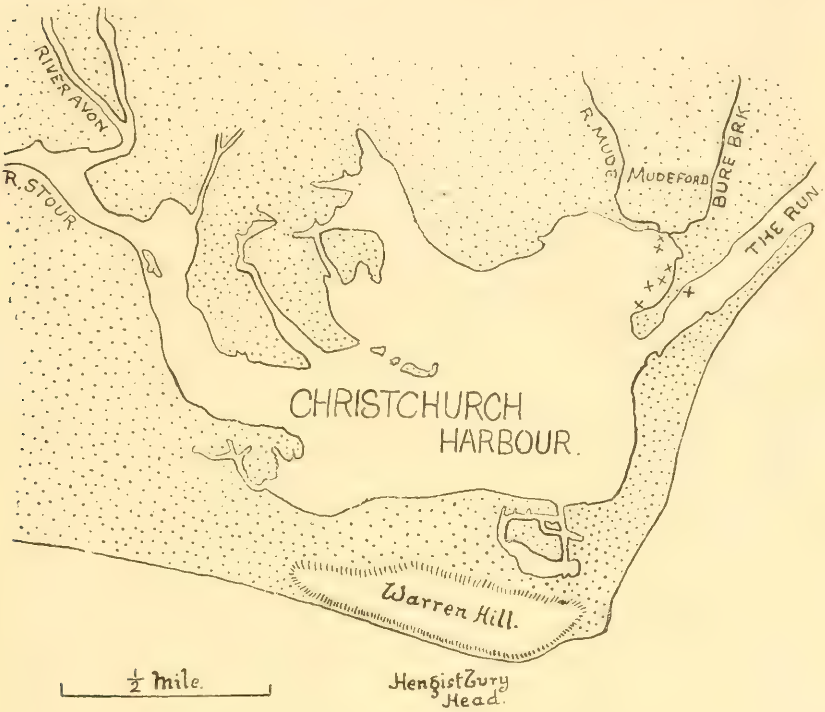
[1] A. De Candolle, *Géographie Botanique*, 1855, p. 1053.

[2] E. F. Linton, *Flora of Bournemouth*, p. 246.

[3] For a summary of records of the distribution of *Spartina Townsendii* and its allies, see O. Stapf: Mud-binding Grasses, *Kew Bull.*, 1907, p. 190; Gardener's *Chronicle, Spartina Townsendii*, 1908, p. 33; Townsend's Grass or Rice Grass, *Proc. Bournemouth Nat. Sci. Soc.*, Vol. v, 1913. For Poole Harbour, see R. V. Sherring's three Spartina Reports in *Proc. Bournemouth Nat. Sci. Soc.*, Vols. v, vii and ix.



Text-fig. 1. Sketch map of Christchurch Harbour (Hants.) showing the distribution of *Spartina Townsendii*, Nov. 1919. The clumps are marked by crosses, × ×. The first plant to settle was the one in The Run (1913); it is now 6 ft. across and is seen in the foreground of Pl. II, fig. 1. Land surfaces not covered by ordinary high tides are dotted. Charted by the Rev. C. O. S. Hatton.

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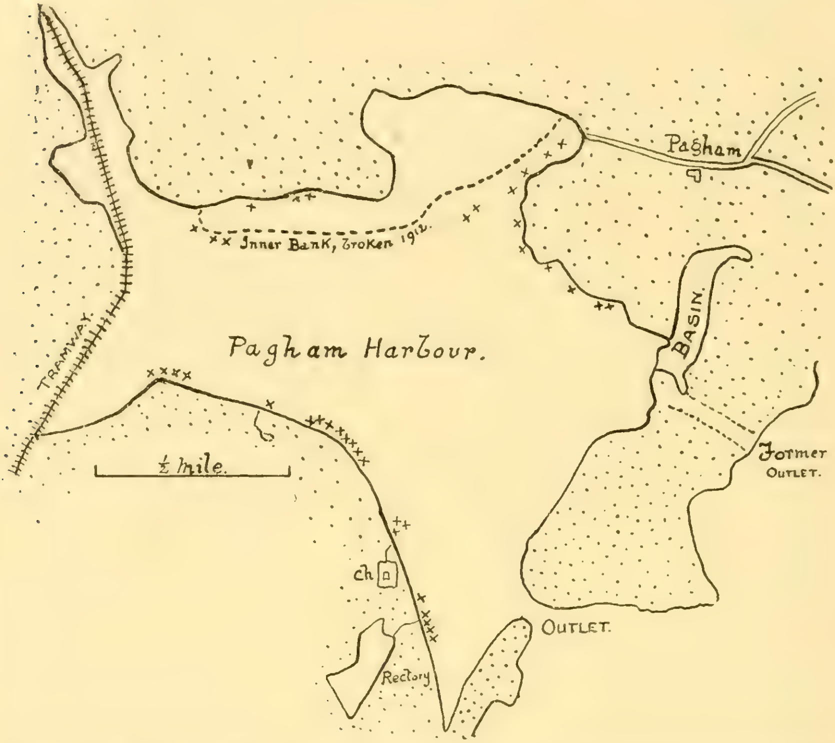
[1] The following notes, from the Rev. C. O. S. Hatton, of Hinton Vicarage, Christchurch, who has kept in touch with this invasion from the first, are of unusual interest. I am much indebted to his courtesy in letting me publish them here.

"The first plant I noticed (and I feel pretty sure it was the first in the harbour) was in a little bit of backwater off the channel which connects the harbour and the sea. It was not at all a good position for it, being constantly covered with dead seaweed, etc. There were only a few blades when I first saw it in 1913, and it did not flower till 1917 when it produced two spikes. Having by that time grown high enough not to be constantly covered with rubbish it grew more quickly, and in 1918 there were about two dozen flower spikes and this year [1919] it flowered well and is now a circular clump about 2 yards across (cf. Fig. 1, Pl. II). I noticed one or two other clumps in the harbour in 1918 and this year [1919] I counted five others, growing well, also a good deal growing amongst other vegetation on the E. side of the harbour. The part where the new patches have sprung up is an ideal situation and I have no doubt that in a few years it will cover many acres of the present harbour. I should say that Christchurch Harbour is even more suitable for the Spartina than Poole and I shall be surprised if it does not spread even faster there."

Langston and Chichester Harbours have been long in occupation, Spartina has at length rounded Selsey Bill and got a footing in Pagham Harbour—though as recently as 1917 none was reported by botanists searching these muds. Apart from introductions for experimental purposes, referred to at p. 35, the above cover all known British localities to which the plant has spread by natural agencies. Some ten years ago it was reported as having reached the French coast (Rivers Saire and Vire in the Cherbourg peninsula) but no further information as to its spread in France is available[1].


Pagham
Inner Bank, broken 1912.
Pagham Harbour.
Tramway.
Basin.
Former Outlet.
½ mile.
Ch
Rectory
Outlet.

Text-fig. 2. Sketch map of Pagham Harbour (Sussex) showing the distribution of *Spartina Townsendii*, Nov. 1919. The clumps are marked by crosses × ×, and are mostly about 2 ft. in diameter. Land above tidal range dotted. Charted by Dr and Miss Barford.

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[1] O. Stapf, *Townsend's Grass or Rice Grass*, p. 5 of reprint.

THE ORIGIN OF *SPARTINA TOWNSENDII.*

This species of Spartina is unknown anywhere in the world except at Southampton, where it originated, and in the adjacent waters which it has since invaded. There is no reason therefore for regarding it, like *S. alterniflora,* as an introduced plant. On the contrary, it must have been produced *in situ.* The current hypothesis, though not yet scientifically grounded, is that *S. Townsendii* is a naturally produced hybrid between *S. stricta* and *S. alterniflora.* This view we owe to Dr O. Stapf who has also made available a great deal of botanical information bearing on the plant.

This hypothesis is strengthened by the fact that at the mouth of the River Adour, near Bayonne, where, as at Southampton, *S. stricta* and *alterniflora* also occurred side by side, a new form named *S. Neyrautii,* having much in common with *S. Townsendii,* has appeared. The presumption is of course that both forms are spontaneous hybrids which have appeared at the only spots where such a thing was possible, i.e. at the only known spots where the two parent forms occurred together.

In support of the hybrid nature of *S. Townsendii* the extraordinary vigour of its growth and spread may be cited. In this connection attention has recently been drawn by Dr Augustine Henry to the hybrid nature of not a few forest trees of great vigour of growth and large output of timber. Dr Henry was so much impressed by the matter that he has engaged in the experimental production of hybrid trees with a view to providing forms suitable for use in afforesting the British Isles[1].

On the other hand if *Spartina Townsendii* is really a first cross and if, as seems almost certain, it is largely propagated and spread by seed, it is surprising that there is no evidence of segregation, i.e. of separation into the parent forms.

This anomaly needs clearing up, and, now that it is of general interest, it is much to be hoped some competent plant breeder may be disposed to take up the matter experimentally.

OCCURRENCE AND ECOLOGY.

The ground on which Spartina thrives best is the soft mud flats within 3 ft. of high water mark, such as are characteristic of Poole Harbour and Southampton. Prior to its appearance these flats were extensively occupied by the sea grass (*Zostera*), the ribbon-like leaves of which lie prone on the mud. With the advent of Spartina as the tufts close together Zostera is annihilated, the principal representative of the associated ground vegetation being a small form of the alga Enteromorpha. The higher levels of the flats are the first to be colonised. At first single isolated plants appear, presumed to be seedlings; each plant spreads laterally by means of stolons to form a circular or oval patch; the rate of growth in any direction being from 2–3 ft. per annum under favourable conditions. In this way the expanding tufts soon unite into strips with open passages between—like a jigsaw puzzle approaching completion—and finally meadow into practically continuous stretches covering acres of mud (cf. Pl. II, fig. 2).

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[1] A. Henry, The Artificial Production of vigorous trees, *Journ. Dept. Agr.,* Ireland, Oct., 1914.

In their earlier stages the height of the grass shoots is uniform over the patches, but as they expand (e.g. at 5–6 ft. diameter) the patches become saucer-shaped owing to the haulms of the central, older parts falling short of those at the periphery[1]. With the further extension of the patches this marginal effect, though still persisting, becomes less noticeable.

The height reached by the grass in its growth varies from season to season, depending particularly on the rainfall in the earlier part of the summer. In this respect Spartina resembles Salicornia and the other halophytes of the salt marsh. Flowering is spread over a long period (July–November) with maximum in September. It is stated to be a shy seeder in most seasons, with occasional bumper years.

Spartina roots very freely from its underground stems. There are two types of root: (1) long, anchoring roots which descend unbranched in the mud for 2 or even 3 ft.; (2) short, branched, superficial feeding roots, so closely crowded together as to form a continuous plexus in the surface layer (cf. Fig. 3; the sketch is reduced to $\frac{1}{3}$ nat. size).

A marked effect of Spartina is the collection and holding of suspended mud. The rise in level from this cause will sometimes reach as much as 4 or 5 inches in a year, though it is not implied that this rate of accretion is maintained indefinitely. The presence of the plant has a marked stabilising effect on the mud, so much so that it is possible to walk about on the meadows in relative safety.

Except where the Spartina meadows approach the shore they form pure stands, free from invasion by other halophytes. It seems too early to say whether Spartina is destined ultimately to give place to other vegetation, though judging from analogous cases such replacement may be regarded as probable. Should such a succession occur there is no

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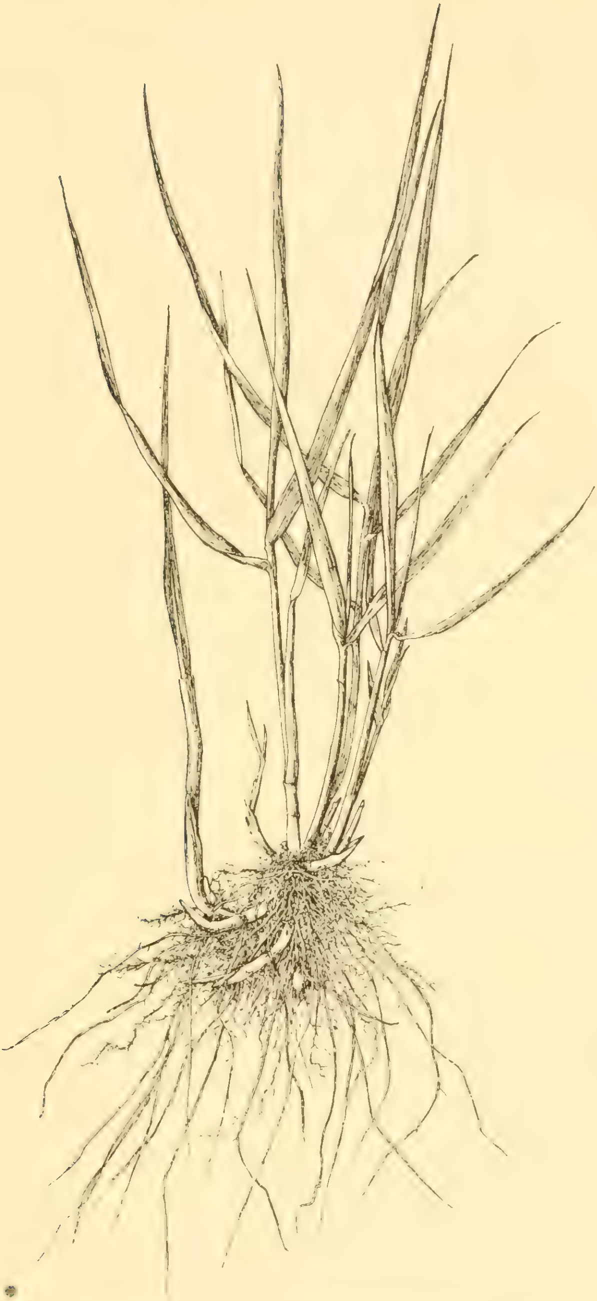
[1] At the present time this "marginal effect" is well shown by numerous patches of Spartina in Holes Bay bordering the L.& S.W. Railway to the west of Poole Station.



Text-fig. 3. Young ? seedling plant of *Spartina Townsendii*, not yet in the flowering stage (Nov. 1916). At the base, several stolons emerging from dense felt of surface roots; lower down are the long anchoring roots which may reach a depth of 2–3 feet.

reason to suppose that the saltings built up by Spartina would degenerate or yield up the mud which had been accreted. The Spartina would have done its work.

During the summer of 1919 a certain number of Spartina plants have been washed out of the mud of Poole Harbour and drifted down to the mouth. As these plants are quite intact they can only have been loosened by lateral erosion—due probably to some migrating creek undercutting one of the meadows. This is an ordinary occurrence on every salt marsh and cannot be made the ground for supposing that any general disappearance of Spartina is foreshadowed.

Near the shore line Spartina often comes into relation with *Scirpus maritimus*, *Juncus maritimus* and *J. Gerardi*, the meadows closing in and cutting off the free connection of these plants with open waters. Cases have been observed (e.g. to the west of Fitzworth Point, Poole Harbour) where Scirpus thus surrounded is dying wholesale—a result which may be due to competition, though it is premature to dogmatise. On the other hand where Spartina meets *Juncus Gerardi* (as at the head of Brands Bay, Poole Harbour) the latter, to judge from appearances, seems quite capable of holding its own.

From this slight sketch of the ecology of Spartina it is evident much remains to be done in the way of field observations of all sorts. Not only are the details of the life history largely unknown—it is doubtful if the history of a single plant of Spartina has been traced from the seedling or gemmule stage to the established clump. The relative importance played in distribution by seed and detached vegetative fragments has still to be ascertained.

It is evident that intensive work of this kind can only be done locally by persons on the spot. From the special nature of the habitat Spartina studies are an acquired taste. Every visit to a clump requires the use of mud boards on the feet, whilst the occurrence in these waters of four tides a day circumscribes opportunity of access.

Great value attaches to the systematic records of the spread of Spartina in Poole Harbour which Mr R. V. Sherring has undertaken. It is much to be hoped that his copious notes and photographic survey of the yearly advance may be published in collected form.

ECONOMIC ASPECTS.

The appearance on our shores of a new and vigorous plant like Spartina with its great capacity for accreting mud and its promise of indefinite spread raise the vital question of its probable effect on navigation in the waters concerned; in addition there are several economic applications to which Spartina may lend itself.

1. Navigation.

Though other navigable waters will doubtless be involved it is convenient to restrict the present discussion to the case of Poole Harbour, where Spartina has been steadily spreading for 20 years.

After the object lesson of the great war no one is likely to question the assertion that it is a national interest that Poole Harbour should remain a place primarily for ships and fishermen. And yet the idea of extensive reclamation is hard to resist in view of the great Spartina meadows which are everywhere appearing. As a Poole fisherman put it, after helping to harvest a sample of the grass for a paper making trial, "You'll see, me and my brother will be farmers yet."

The danger to navigation inherent in reclamation is this. When parts of a tidal estuary are banked off and removed from tidal action, by so much is storage space for water diminished; and this amount will be lacking for scour at the ebb. The result is that the channels become choked and navigation suffers.

Suppose for example five square miles of the estuary carrying on the average a depth of 2 ft. of water at the spring tides to be banked off. This would mean a deficit of about 280 million cubic feet—a volume of water far from negligible in this connection. The history of not a few decayed ports shows that there exists eternal antagonism between agriculture and navigation. When prices of produce rule high the land tends to encroach on the waters. The immediate gain is obvious and tangible, the ultimate consequences remote and shadowy. Amid a multiplicity of authorities the frontagers are apt to help themselves unless the community is unusually vigilant.

No one can foretell with absolute certainty what will happen as a consequence of the spread of Spartina. There is an unknown factor, the persistence of this new invader. At the same time there are no signs of respite and it will be safest to assume the worst.

The action of Spartina may be pictured as follows. The plant spreads rapidly on the mud flats and tends to fix such mobile mud as may be drifted over it. In this way in proportion as the flats are colonised by Spartina their level rises.

The immediate source of the mud which Spartina is fixing will be the sides and bottoms of the channels, though a certain very small amount of this will be made good by new mud entering the harbour by the rivers which discharge into it. In its present phase Spartina has an insatiable appetite for mud with the result that much mud is being transferred from lower to higher levels. As the new mud entering is almost negligible in amount what is taking place is substantially of the nature of a redistribution of mud already present.

Corresponding to this phase a widening and deepening of the channels is to be expected, an assumption which appears to agree with local observation.

As time goes on and the Spartina spread approaches its limits the rate of assimilation of mud in the higher levels will be abated. The early hunger for mud having been satisfied the final rise in level (as the height of the flats approaches the limits of tidal rise) will be much more gradual than in the preceding phase.

Following such a redistribution of mud, two consequences are to be expected. (1) Owing to the increased sectional areas of the channels the rate of flow would be slowed and (2) the tidal water, being largely displaced by mud in the higher levels, would occupy on the average a lower level than was the case before the advent of Spartina.

Both these effects, i.e. the slowing of the currents and the lesser head of tidal water should work towards a diminution of scouring power at the ebb. The mouth would thus tend to become encumbered with silt to the impairment of navigation.

But Poole Harbour is singular in its construction from the extreme narrowness of its mouth. The area of the harbour is roughly 20 square miles, whilst the outlet is only 350 yards wide. As a consequence the harbour is stated never really to fill at high tide, i.e. to reach the full height to which it is potentially entitled, because the tidal wave outside passes the mouth too quickly.

Based on the existence of a substantial difference in level between high tide within and high tide without, the theory obtains locally that, after all, Poole Harbour may prove immune to the usual consequences of excessive silting. As the Spartina completes its work and the mud is transferred from the bottom to the top, the tide will have less far to go and will no longer waste the precious moments in excessive lateral travel. On the contrary it is expected by local optimists that in fulness of time the tide will rise in the channels to an appreciably higher level than it does at present. Hence it seems to follow that, taken in connection with the unexhausted head of water outside, Spartina is to be hailed as the regenerator and not as the probable destroyer of the régime of Poole Harbour. In other words the one thing required to remove the defect of a harbour too big for its mouth was the arrival of just such a vigorous agent of reclamation as Spartina is proving itself to be!

The dissemination of this theory in its unproved state is dangerous if not vicious. It is one of those comforting theories which beguiles human nature into sitting tight and doing nothing. It is much more agreeable to "wait and see" than to take the arduous but necessary steps towards finding out. Spartina has now been encroaching for 20 years and systematic observations should reveal whether the trend of change is in the direction implied by this theory. Meanwhile, what is the experience with other narrow mouthed harbours? Are they immune from deterioration when halophytic vegetation invades their mud flats?

2. SPARTINA AS AN AGENT IN RECLAMATION.

It is obvious that a vigorous plant like Spartina, capable of colonising soft and mobile mud flats, must have considerable value from this point of view. In Britain roots have been transplanted to a number of localities with a view to studying the behaviour of Spartina under varying surroundings. Among these may be mentioned the Firth of Forth, Wells (Norfolk), and the Harwich estuary. At Clevedon (Somerset)[1] and Sheerness it has been planted with the definite object of protecting the coast line from erosion by scour, and with considerable success, so it appears. Further afield consignments have been sent to New Zealand, Australia, S. America and other distant spots, and when the time is ready it is much to be hoped that a collective report may be prepared detailing the results of all such experiments. The notice which Spartina as a reclaiming agent has received from overseas is noteworthy and the demand appears to be increasing. It will perhaps be convenient to state here that Lord Montagu of Beaulieu is always willing to deal with applications of this kind.

3. AS A FEED FOR STOCK.

No one who has lived on a farm, bordering e.g. on Poole Harbour, can have remained in doubt as to the value of Spartina in the feeding of stock. Horses, sheep and cattle eat it with avidity and habitually make their way on to the Spartina meadows almost before the tide has run off. Farmers speak well of it except that it gives an undesirable flavour to milk. As the grass remains standing on its roots throughout the winter till April, it forms a most convenient reserve feed that can be cut as required.

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[1] According to information from Miss I. M. Roper.

So far as we know analyses have not been published, nor proper feeding trials conducted. It is desirable that both these matters should be put through and the results made known. On the coast of New England related species of Spartina are regularly harvested and the hay fed to cattle[1].

4. As a Raw Material for Paper.

The presence of a tall growing grass like Spartina in pure stands of almost unlimited extent suggested the possibility of its employment as a paper-making material. A preliminary sample was submitted to the late Mr Clayton Beadle, the well-known paper expert, in July 1916, and as a result of his encouraging report steps were taken to collect larger samples for trial at a paper mill.

With the approval and assistance of the Poole Harbour Board large cuts of Spartina were made in October 1916 and in March 1917. These were forwarded to Messrs Thomas and Green, Paper Makers, who converted them into paper at their mills at Wooburn in Bucks.

The October cut was sent green and wet and after washing at the mills, was boiled wet.

The March sample was dried as well as the conditions at the time allowed and was boiled dry.

Both samples contained a good deal of mud which could not be altogether removed by mechanical means and persisted as black specks in the paper.

By the summer of 1917 labour being unobtainable at Poole, a squad of boys and girls from Oldfeld School, Swanage, was organised by Mr B. K. Hunter for an August Spartina camp at Ower on the Studland side of Poole Harbour. This camp was repeated in August 1918.

The work of these camps consisted in mowing and bringing the grass ashore, washing it and picking out the dead stalks of previous seasons, transporting it to the drying ground where it was spread out in the sun, and when dry sacking it and getting it on to the rail.

As these two cuts from the Ower camp do not together make an economic sample for boiling (about 4 tons dry weight) they are being kept in store till the balance can be sent. In 1919 it was not possible to hold a Spartina camp but it is hoped in 1920 that the job may be completed.

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[1] F. Lamson-Scribner, Grasses of Salt Marshes, *Yearbook U.S. Dept. of Agric.* 1895, p. 324.

In spite of this postponement, several additional small samples have been treated, and a great deal of experience gained in methods of harvesting, etc.

The notes which follow are provisional conclusions based on the experience of 1916 to 1918.

(1) *Harvesting.* The proper time to cut the grass is in August when it has reached its full growth, and whilst there still remains probability of several weeks drying weather. It is best cut with a scythe a day or two before the spring tides. The grass should be left in swaythes just as it falls and not carried ashore. The spring tides will float it, and if the area cut be surrounded by corked ropes or spars lashed together the cut will not drift beyond this enclosure which can be towed to some convenient spot at high water.

The grass will be efficiently cleansed of mud by the scour of the tide as it runs through it so that special cleaning by hand is superfluous.

In the case of areas not previously cut many old haulms of previous years are mingled in the current growth. These have to be picked out by hand before the grass is spread out to dry, as old rotten fibre spoils the paper pulp. The labour involved in this operation is enormous. If one man can pick a stone of wet grass (i.e. separate the current growth from that of previous years) in an hour it will require 160 man hours to pick over a ton. In other words the picking over of this amount is a week's job for four men of the "casual" order. Trained labourers would of course work much more rapidly. This picking is the limiting factor in harvesting Spartina and accounts for the small output of our Spartina camps. One man can mow in two days more grass than 12 boys can pick over in a week.

However, should Spartina ever be regularly exploited the need for this operation of picking over will disappear. For when an area has been cut, next year's crop will be free from old stalks and can be harvested in its entirety. Small experimental areas have been cut for three successive years and we find no appreciable diminution of the yield: at any rate the fluctuations are within the range of purely seasonal factors. So that it comes to this. The cut after the first year can be taken entire and can be freed of mud by letting the tide scour it. No hand labour is required other than that involved in mowing and transporting the cut to the drying grounds. A good yield would be two tons (dry weight) per acre. Whether it may not be desirable to let an occasional year pass without cutting we are unable to say. There is always a danger of overcropping, and if exploitation should be undertaken the matter will have to be carefully considered[1].

Our experience of drying is confined to natural means. Spread out on exposed wind-swept ground in fine weather (August and September) the cut should be dry in three weeks. If through broken weather it is still wet by the middle of September there may be difficulty in saving the crop. Drying is hastened by arranging the grass in little stooks or resting it against brushwood or hurdles. On the whole with vigilance and judicious handling the crop should be capable of natural drying three years out of four. But the possibilities of artificial drying deserve serious consideration.

(2) *Conversion into pulp.* In the trials hitherto carried out the Spartina fibre has been boiled and bleached according to the standard treatment for esparto. Though the pulp possesses distinctly useful qualities in paper-making we prefer to speak here of some of its shortcomings, as the correction of these is a necessary preliminary to its adoption. Some of these are uncurable, such as the yield, which averages 30 per cent. on the dry weight of fibre boiled. This defect it is to be hoped may be compensated by the purity and density of the stands, the relative ease of harvesting and the proximity of the home market. Meanwhile there is the difficulty of bleaching the pulp to a satisfactory colour. Until this is solved by a special chemical research it is hopeless to think of Spartina as a material for fine papers. Should the bleaching problem prove insoluble *Spartina Townsendii* could probably be converted into straw boards as was the related American slough grass (*Spartina michauxiana*) at Quincy in Ohio.

Another trouble concerns the hydration of the pulp; Spartina-pulp is rather apt to "run wet" on the paper-making machine, a defect which may depend (as some experts suspect) on its marine origin—a new factor in the origin of these raw materials. These and other matters of like nature will have to be smoothed out before Spartina can take its place in the paper industry, just as must always have been the case with other raw materials in this and other industries. Whatever may come of the present project it is hard to believe that at some future time, when Spartina has spread into all the muds of our shores, this plant will not find a use in the paper-making world. Allowing for an average yield of two tons dry weight per acre enough Spartina is already present in these waters to feed a mill all the year round with 100 to 150 tons per week.

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[1] The collection of esparto grass is carefully regulated in this sense. Cf. H. de Montessus de Ballore, *Alfa et papier d'alfa* (Dunod and Pinat, 1909), p. 9.

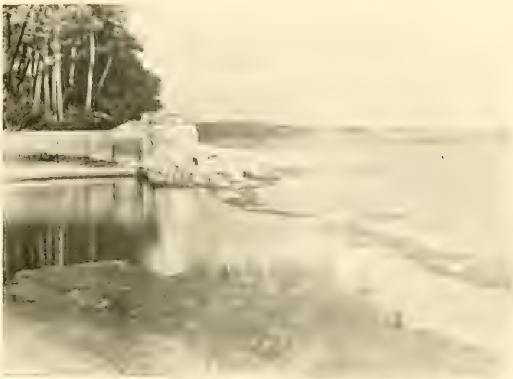

Fig. 1.

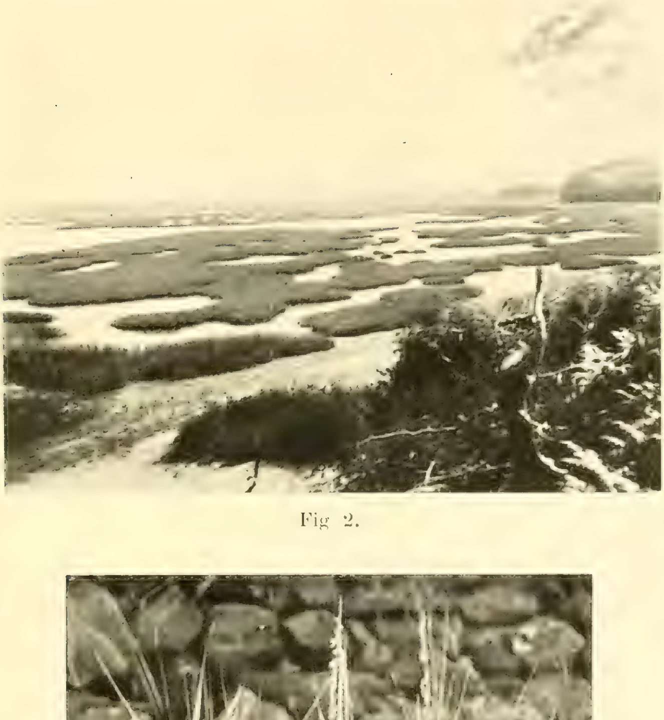

Fig. 2.

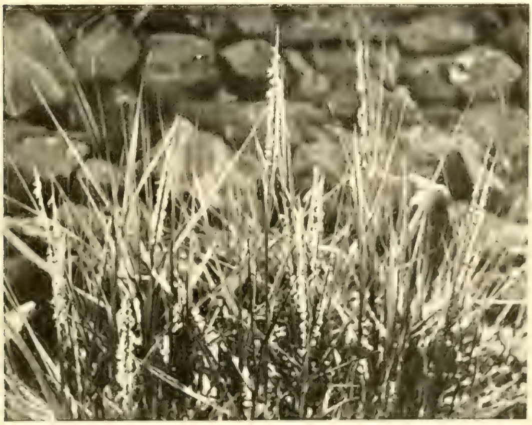

Fig. 3.

Other uses for Spartina are sure to present themselves as knowledge increases of the ways in which plants may be chemically exploited for particular purposes. The important points in the present case are the extent, purity and density of the stands, combined with relative ease of cutting and transport.

Really in Spartina we have a subject that seems to call for facilities for investigation such as can only be provided by what for want of a better name may be termed a Spartina Institute located on the spot.

From every point of view full knowledge is required, alike whether the plant be regarded as a botanical phenomenon, a weed which seriously threatens navigation, or a gift of providence capable of being put to a variety of uses.

DESCRIPTION OF PHOTOGRAPHS ON PLATE II

Fig. 1. The original clump of *Spartina Townsendii* which established itself in 1913 on the north side of the outlet of Christchurch Harbour. Longest diameter of clump 6 ft. Photo. taken Nov. 1919 and communicated by the Rev. C. O. S. Hatton.

Fig. 2. Spartina field in Brands Bay, Poole Harbour, showing a characteristic phase in colonisation. Taken from the south side of Goathorn Point looking S.W. E. J. Salisbury, photo. Aug. 1919.

Fig. 3. Clump of Spartina in flower. The white appendages are the stigmas. E. J. Salisbury, photo. Aug., 1919.

INVESTIGATION OF THE NATURE AND CAUSE OF THE DAMAGE TO PLANT TISSUE RESULTING FROM THE FEEDING OF CAPSID BUGS.

By KENNETH M. SMITH, A.R.C.S., D.I.C.

(*Adviser in Agricultural Entomology, Manchester University.*)

(With 1 Plate and 5 text-figures.)

This piece of work was suggested by Mr J. C. F. Fryer, entomologist to the Ministry of Agriculture and was carried out at the Royal College of Science, S. Kensington, under Prof. H. Maxwell Lefroy.

I wish to acknowledge my indebtedness to Prof. Blackman and Dr S. G. Paine, of the Imperial College of Science and Technology, for much valuable assistance and advice.

The object of this investigation was to discover the causes of the damage to plants and especially to apple trees from the feeding of Capsid bugs. There are many species of Capsids which normally feed on the fruit and leaves of apple trees in this country, those which have attracted most attention being the following: *Plesiocoris rugicollis*, *Atractotomus mali*, *Orthotylus marginalis* and *Psallus ambiguus*; only the first-named causes any damage to the fruit and foliage (Fryer(1), Petherbridge and Husain(2) and others). *Lygus pratensis* also is found by Collinge(3), to cause damage to the apple fruit itself by depositing its eggs in the lenticels, but not by sucking the juices. The problem to be solved is, then, as follows. There are four species of Capsid bugs, mostly closely allied, all feeding on apple fruit and foliage and feeding by the same process, i.e. by inserting their mouth-parts into the tissue and sucking the sap, yet only one of them, *Plesiocoris rugicollis*, causes any damage.

P. rugicollis hatches out in May, and the young Capsids immediately begin to feed voraciously, picking out the young shoots which soon become covered with spots and patches of dead cells; this has the effect of keeping back the shoots and young leaves to a very large extent, and in some cases causes the death of the whole shoot. When the young apples begin to form, the Capsids transfer their attention to these, which in their turn become rapidly covered with red spots, each spot, of course, marking the point of insertion of the stylets. Thus far the injury to the apple appears identical with that of the leaf, but after a short time the apple becomes cracked, a corky layer is formed, and a very distorted fruit results; in many cases the badly attacked apple ceases to grow and falls off. This is in marked contrast to the other three species mentioned above which feed in a similar manner and yet produce no ill effects whatever. The question then arises, what is there about this particular species in contrast with the others, that the sucking action should be followed by so lethal an effect upon the tissues of the foliage and fruit.

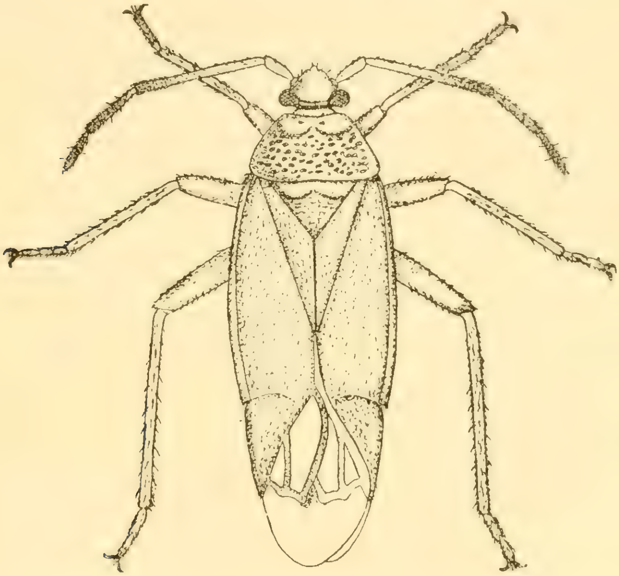

Fig. 1. Adult specimen of *Plesiocoris rugicollis.* After Petherbridge and Husain.

When this bug has sucked some of the sap, which it does by pushing its sharp stylets into the tissue and drawing up the liquid by means of a powerful pump situated in the head, at the same time injecting saliva into the wound (Awati (4)), the stylets are withdrawn and inserted elsewhere, meanwhile a drop of fluid gathers at the first puncture gradually getting larger as the cells are killed and yield up their contents. When this drop has dried up, the cells underlying it are all killed leaving a large discoloured patch which may continue to spread slightly especially if in the neighbourhood of a vein.

In the case of the apple fruit these dead cells present a dark red or brown appearance owing to the formation of a tannin which gives a black coloration with ferrous sulphate. Microtome sections of portions of apple leaf injured by *P. rugicollis* show a mass of dead cells filled with a red granular material, the epidermis dying after the mesophyll, this confirms Petherbridge and Husain (2). When *P. rugicollis* feeds on Willow a clear space is produced round each puncture so that if damaged by several punctures the leaf becomes transparent and dies. Sections of such a leaf show that the cells are killed and filled with a clear substance very similar in appearance to that found in the cells of the apple, so that the reaction appears identical with that produced in the apple, with the exception of the colour reaction. The production of the red-brown pigment is merely a death phenomenon of the apple cells and is no special reaction to the Capsid; apple leaves if held in chloroform vapour produce the same red pigment.

We come now to consider the possible explanations of this damage. These seem to be three:

Firstly, a purely mechanical injury caused by the laceration of the tissues by the stylets in process of sucking.

Secondly, the possibility of the bug acting as a "carrier" of bacteria and injecting them into the plant along with the salivary juices and so setting up a pathological state. An interesting parallel to this is found in the case of the Beet Leaf hopper which carries the germs of beet curly top (Stahl and Carsner (5)).

Thirdly, the injection of some secretion, either from the salivary glands, which is the more probable, or a regurgitation from the stomach which has a virulent toxic effect on the tissue. These three theories seem to cover the only possible explanations of the damage. As has been mentioned already, the formation of the red brown pigment is a death phenomenon of the apple and it is possible by means of laceration with a sterile needle to produce a small brown spot similar in appearance to that produced by the Capsid but not approaching it in extent of the injury. The following attempts were made with sterile needles of varying fineness to reproduce the injury caused by the bugs.

(1) Scratch on the surface of the leaf with a dry sterile needle.
(2) Puncture with dry sterile needle.
(3) Scratch through sterile water.
(4) Puncture through sterile water.
(5) Puncture with dry needle not penetrating the leaf.

In each case only cells actually lacerated by the needles were killed, the injury did not spread and the leaves were not put back in their development.

If it is assumed that the injury is due to the mechanical laceration of the cells and their consequent loss of sap by the stylets of the bug, then the question arises, why do not the other species of apple feeding bugs produce the same effect? as the methods of feeding, and the mandibles and maxillary stylets are precisely the same in each case.

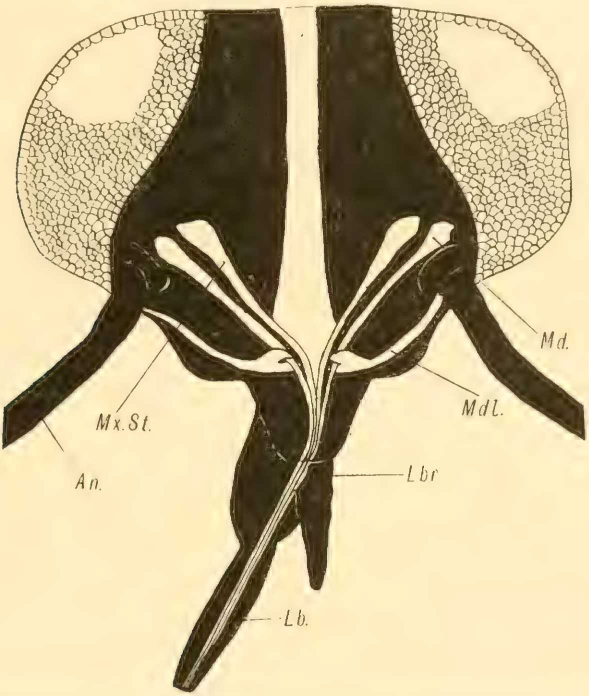

Fig. 2. Semi-diagrammatic drawing of the head of *Lygus pabulinus* showing mouth parts.

Attempts were made under the binocular microscope to pierce the leaf with the mouth-parts of various species after they had been removed from the head so that there was no possibility of any salivary juices being injected: this was not very satisfactory owing to the extreme fineness of the stylets, but in a few instances perforation was effected but with no visible results, the stylets apparently being too minute to kill more than one or two cells by laceration. As regards the possibility of the loss of sap by sucking causing the damage, if this were so it would of necessity follow that all the species of Capsids and indeed any sucking insect should produce similar harmful results.

Taking all these facts into consideration, it will be seen that mechanical injury alone is not sufficient to account for such serious damage.

Turning now to the second possible explanation, that of injection of bacteria with the salivary juices, the following experiments were made to decide this point:

Very thin microtome sections of the salivary glands of *Plesiocoris rugicollis* and one or two other apple feeding bugs were cut in order to verify if possible, the presence of bacteria in the glands and ducts; the sections were stained with various bacterial stains, such as Victoria Blue, Carbol Fuchsin, Gram's Stain etc., but in no case were there any indications of bacteria. Sections were also cut of the damaged portions of apple and willow leaves and stained with various bacterial stains as above, in order to trace bacteria in the cells. Although some of the cells presented a slightly granular appearance, this was found to be due to the presence of the tannin and no bacteria could be discovered. Apple leaves badly damaged by *P. rugicollis* were then taken and ground up with sterile sand in a mortar under sterile conditions with the addition of a little sterile water, the resulting extract was allowed to stand and the clear red fluid drawn off, it was then injected with a sterile hypodermic syringe into undamaged apple and willow leaves. A solution of damaged willow leaf was made under similar conditions and also injected into apple and willow leaves.

The inoculations made were as follows:

(1) Inoculation of apple leaf with sterile water control.

(2) Inoculation of apple leaf with extract of damaged apple leaf.

(3) Inoculation of apple leaf with extract as in (2) but boiled.

(4) Inoculation of apple leaf with a similar extract of willow leaves damaged by the same insect.

(5) Inoculation of apple leaf extract as in (4) but boiled.

A certain amount of damage was produced in each case, very slightly more marked in (2) and (4) than in the others. Five precisely similar injections were then made into willow leaves, these gave negative results, only such cells as actually came into contact with the hypodermic needle apparently being affected.

Bacterial cultures were then made from the damaged leaves as follows. The leaves were ground up as before with sterile sand and sterile water under sterile conditions and a drop of the resulting fluid was added to 10 c.c. of sterile water and plated out on various media, Turnip Agar + 4, Potato Mush Agar, Beef Agar, etc., after five days many small round colonies were observed, these were plated out until a pure culture of a bright chrome-red organism was obtained. A number of the harmless apple-feeding Capsids in a starved condition were then introduced into a petri dish containing the above culture; after they had all been observed to insert their stylets into the medium and to be well plastered with the colonies, they were transferred to a fresh young apple shoot and allowed to feed, no damage resulted. Suspensions were then made of the colonies and injected by means of a sterile syringe as follows into both apple and willow leaves:

(1) Sterile water control.

(2) Suspension of living bacteria.

(3) Suspension of dead bacteria (boiled).

A larger area of damage was caused by (2) and (3) than by the control, there presumably being a toxin present due to the presence of the bacteria in the injection, but as the damage caused by (3) was precisely similar to that caused by (2), it cannot be taken as evidence that bacteria are the cause of the injury under investigation.

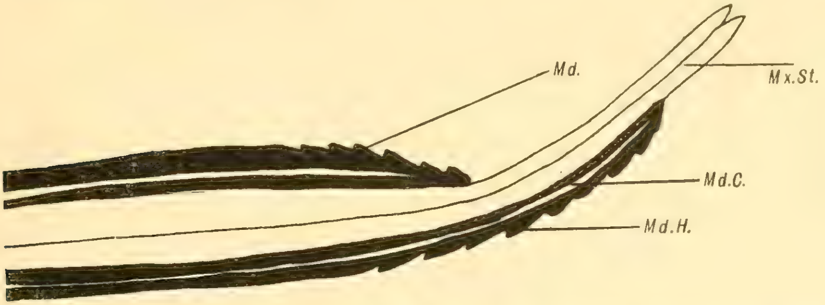

Fig. 3. Mandibles and maxillae of *Lygus pabulinus*. Drawn with the camera lucida, under the $\frac{1}{12}$ oil immersion, ocular 4.

Inoculations were then made with a number of common bacterial saprophytes, including the red organism already mentioned, in order to find out if any of them would continue to live saprophytically in the plant tissue if entrance were made for them, either artificially by the needle or by the Capsid's stylets, and if so, whether they would produce damage similar to that known to follow the feeding of *P. rugicollis*.

The following inoculations were made into apple leaf:

(1) Suspensions of the red bacteria isolated from the damaged apple leaf.

(2) The same with dead bacteria.

(3) Suspension of *Bacillus mesentericus*.

(4) Suspension as in (3) but boiled.

(5) Suspension of *Bacillus vulgaris*.
(6) Suspension as in (5) but boiled.
(7) Suspension of *Bacillus subtilis*.
(8) Suspension as in (7) but boiled.
(9) Suspension of *Bacillus mycoides*.
(10) Suspension as in (9) but boiled.

These inoculations were also made into willow leaves. In each case only slight damage was caused, in no way comparable to that produced by the Capsid.

The foregoing experiments seem to prove conclusively that bacteria play no part in producing the damage resulting from the feeding of the bug. The fact that the insects from the moment of hatching produce the same damage as the adults, also militates very strongly against the theory of bacterial infection as it would necessitate the bacteria passing on from generation to generation and also their having to pass the winter in the egg. The chrome-red colonies of bacteria which were isolated from the damaged apple leaf were presumably merely living on the surface and had no connection with either insect or damage.

There is left now the third possibility, i.e. that the salivary secretions injected into the tissue have a toxic effect. There are known to be two ducts (Awati (4)) down one of which there passes the salivary juices while up the other passes the plant sap, presumably mixed with some saliva. The saliva is injected under pressure by means of the very powerful pump situated in the head of the insect. After the leaf has been punctured and the insect's stylets withdrawn, a drop of fluid exudes from the hole and slowly grows in size as the cells below are killed and give up their contents. This is in marked contrast to the prick with a sterile needle or the puncture made by the harmless bugs where no drop of fluid exudes. The theory of harmful salivary injection is certainly the most probable of the three possible explanations, and further observations seem to bear this out.

The salivary glands of Capsids in general consist of a paired bilobed gland (see Fig. 4) situated in the meta-thorax one on each side, from the centre of this runs a long tube with apparently glandular walls, up to the neck where it doubles back again, ending near the gland proper in a very thin walled vesicle or reservoir which is not secretory; a second tube arises at the same point as the first and runs straight to the neck where it connects with the pump. Attempts were made to discover if any morphological difference existed between the salivary glands of *P. rugicollis* and those of other apple-feeding Capsids.

The insects were fixed in Carnoy's fluid (second formula) mostly in the early stages, or after a moult, before the chitin was hard. In spite of these precautions great difficulty was experienced in getting good penetration of the fixing fluid, and it was found necessary to detach the legs or make a small hole in the abdomen for the fixative to gain an entrance. Great care was necessary in embedding in the wax, as too long or too short a time caused the chitin to become too hard and brittle to cut. It was thought possible that the glands of *P. rugicollis* might show some extra secretory cells or that the reservoir itself might prove secretory, but no histological peculiarity was apparent, the salivary apparatus being almost identical in the various species examined, the reservoirs showing as thin collapsed vesicles.

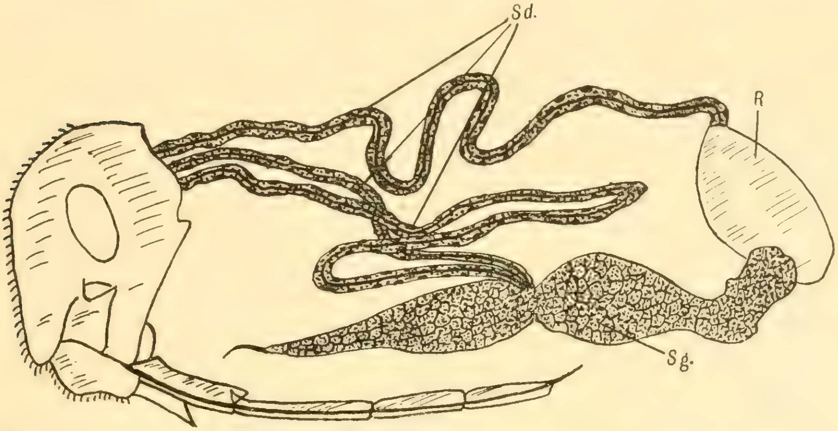

Fig. 4. Semi-diagrammatic drawing of the salivary apparatus of *Plesiocoris rugicollis*. One side only.

The fact of there being no apparent histological differences in the salivary glands of the harmless and harmful bugs does not tell directly against the theory of a toxic secretion, and all other experiments seem to point to this being the true explanation. That the damage to the cells spreads after the bug has moved to another spot, and that the mesophyll dies before the epidermis (except of course where there is a drop of sap and saliva lying on the surface of the leaf) are facts which tell very strongly in favour of this theory. Fig. 4 is a semi-diagrammatic representation of the salivary apparatus of *P. rugicollis*.

Injections were made with various dilute poisons into apple and willow leaf in order to reproduce if possible the damage caused by the bug.

(1) Dilute ammonia.
(2) Chloroform.
(3) Various dilute acids, such as hydrochloric, etc.
(4) Xylol.

In each case the leaf assumed a spotted and patched appearance, very similar to the effect produced by the Capsid, and the leaves were put back in their development to a similar extent, while if pricked with the fluid so that more than 25 per cent. of the area of the leaf was affected, the leaves died. The characteristic red spots appeared on the apple leaves and the clear patches of dead cells appeared on the willow.

The same injections were made into the apple fruit itself, the chief result being the extraordinary retarding effect on the growth of the apple; after a week or ten days the control fruit was twice to three times the size of the pricked fruit, and in many cases the inoculated specimens fell off after ten days or a fortnight.

Further experiments were made to prove conclusively if possible the harmful effects of the salivary juices of *Plesiocoris rugicollis*. A number of the harmful Capsid bugs were ground up in a sterile mortar with a single drop of sterile water and the resulting fluid injected into apple and willow leaves. At the same time and into the same trees, a similar fluid, made from harmless apple Capsids, was also injected, in each case with a sterile water control. This experiment was unsatisfactory, no conclusive results could be drawn from it. A certain amount of damage was done in each case, possibly slightly more in the case of the extract of the harmful bug than in the other, but it seems probable that the harmful substance in the salivary glands was so diluted or neutralised by the other juices of the body or by the sterile water as to lose its toxic effect.

The same experiment was repeated, this time without the sterile water but again with unsatisfactory results.

Finally the whole salivary apparatus was removed from harmful and harmless bugs and pricked into the leaf tissue. This was definitely satisfactory, as the glands of the harmful bug (*P. rugicollis*) were very much more toxic than those of the harmless bug (*P. ambiguus*) which had little or no effect. The salivary apparatus of the injurious insect was placed on a young apple leaf and a small prick with a sterile needle made through it into the tissue beneath. In an hour or two the cells underlying the gland were all killed and by the next morning 50 per cent. of the leaf was dead: a similar prick made through the glands of a harmless Capsid under similar circumstances produced no effect whatever.

As has been mentioned already in this paper the damage to the apple fruit itself is very considerable, owing to the fact that the growth of the apple is almost entirely stopped by the death of the cells of the exterior; in cases where one side only is punctured by the bug, the other side of the apple continues to grow to a certain extent thus causing a greatly distorted fruit.

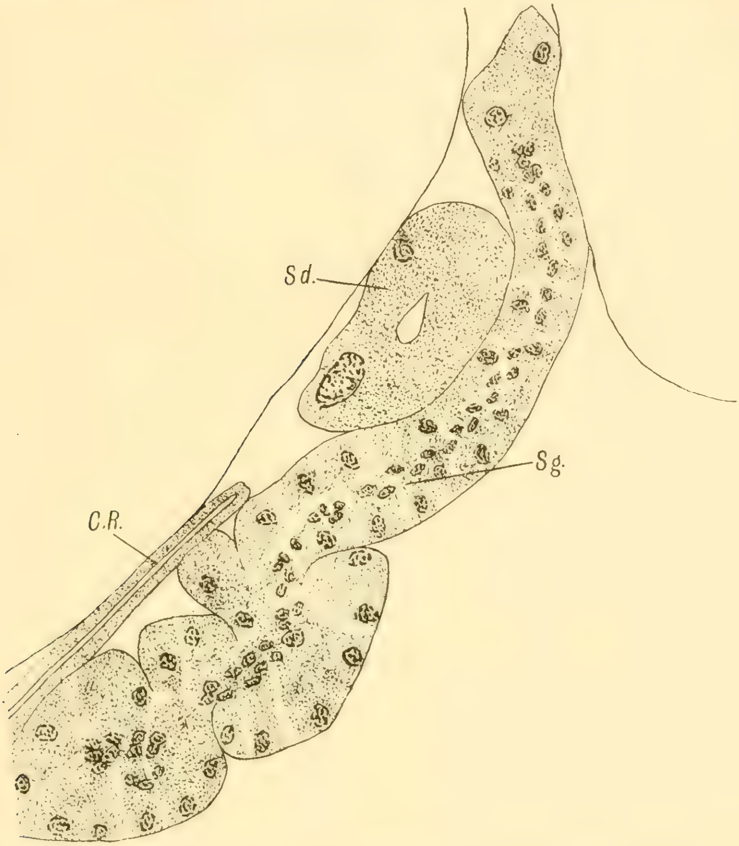

Fig. 5. Section of the salivary gland of *Lygus pabulinus*, 4 μ thick, $\frac{1}{12}$th oil immersion, ocular 4.

When an apple is punctured by the harmful bug, a drop of fluid exudes from the puncture and gradually increases in size, the cells surrounding it are all killed and a corky layer is formed. To investigate this phenomenon further a number of slices of potato were put in damp chambers (Petri dishes lined with wet filter paper) and harmful and harmless bugs introduced.

The object of using potato was to produce the same reaction as in the apple, but on a magnified scale. *Plesiocoris rugicollis*, *Lygus pabulinus* (a species harmful to potato foliage, etc.) and *Psallus ambiguus* were the species used. As soon as the bugs were introduced into the petri dishes they commenced to feed vigorously on the potato slices. From the punctures made by *P. rugicollis* and *L. pabulinus* a small drop of clear fluid exudes, this drop continues to increase in size for two or three hours, by which time it has attained a maximum diameter of about 3 millimetres and become greenish in colour. This drop finally dries up and leaves a large area of blackened dead cells. When the harmless bug sucks the potato no damage is caused to the tissues nor is there any exudation of fluid.

The explanation of the appearance of the drop appears to be that the salivary injection continues to work its way in the tissue till its toxic powers are exhausted, and as each cell is killed its turgidity is lost and its contents exude, forming the large drop as described. It is a striking fact that this exudation should only occur in the case of the harmful bug.

Plate III, fig. 2 is a photograph of potato slices which have been fed upon by the bugs: A and B, by *L. pabulinus*; C, by *P. rugicollis*; and D, by *P. ambiguus*. In A, B and C, will be seen the blackened areas of dead cells round each puncture while in D, although fed upon to a similar extent by *Psallus ambiguus*, there are no harmful results whatever.

The following detailed observations were made of the feeding of *P. rugicollis* and *L. pabulinus* upon potato.

P. rugicollis. *Times after removal of stylets from puncture. Size of drop exuded, in millimetres.*

	1 min.	20 mins.	1 hr.	2 hrs.	3 hrs.	4 hrs.	12 hrs.
(1)	¼	½	¾	1½	2	2½	2½
(2)	¼	½	¾	1–1½	2	2	2
(3)	¼	¼	½	1	1–1½	2	2
Lygus pabulinus	Colourless	Green					
(1)	¼	½	1½	2	3	4	4
(2)	¼	½	1	2	3	2–3	3
(3)	¼	¼	½	1½	2	2	2
(4)	¼	½	1–2	2½	3	3½	3½
(5)	¼	½	1	1½–2	3	4	4

A drop of this exudation was placed upon a young apple shoot; it was found to be decidedly toxic for after a few days the shoot died.

A control experiment of pure potato sap alone had no ill effect upon the apple leaf although left in a damp chamber with the drop of sap *in situ* for several days, thus showing that some toxin had been added to the potato sap and that some chemical change had taken place, this latter as indicated by the change in colour after exposure to the air.

The salivary glands were then taken out of the following species, *P. rugicollis*, *L. pabulinus* and *Psallus ambiguus*, and placed each on the surface of a slice of potato; in the first two cases a large quantity of fluid was produced which gradually oozed out as before, and a large patch of tissue was killed; in the third case there was no effect at all. These drops of fluid were picked up with a capillary pipette and found to be toxic to apple leaves though not apparently to fresh slices of potato.

This seems fairly conclusive evidence that a harmful substance is injected by the bug and that it must be looked for in the salivary glands.

Observations were made of *P. ambiguus* in the act of feeding. Before the stylets are inserted into the tissue the proboscis is held upwards and a large drop of saliva gathers at the end, the proboscis is then lowered and the stylets forced into the tissue through the drop of saliva deposited on the leaf. After the insect has been feeding for some time the surface of the leaf is dotted over with these drops of saliva, these eventually dry up and leave no mark or visible after effect. If these drops are picked up with a capillary pipette and injected into the leaf no damage results, which is in marked contrast with the effect of the drop exuding from the puncture made by *P. rugicollis* which kills the cells underlying it. There appears to be a slight difference in the method of feeding of these two bugs, whereas *P. ambiguus* secretes the saliva and pumps it out before piercing the leaf, *P. rugicollis* inserts the stylets first and then pumps in the saliva, the latter method certainly seems the most effective and it is difficult to account for the deposition of saliva outside the leaf unless this particular species is in the habit of producing greater quantities of the secretion than *P. rugicollis*, and pumps it into the leaf as well.

Sections were cut of tissue, fixed immediately after puncturing by the bug, also of tissue punctured by *P. ambiguus*; these sections did not prove very successful, but punctures were discovered which penetrated some distance and showed laceration of one or two cells.

It is difficult to say how harmless bugs such as *Orthotylus marginatus* and *P. ambiguus* procure their food if their salivary injection does not kill the cells as it seems impossible that the contents of the one or two cells actually lacerated by the stylets should suffice for their needs;

also, if the cells are killed, the characteristic red brown colour should be formed as it invariably is on the death of cells in apple tissue. It was thought possible that *Psallus ambiguus* injected some substance which prevented the formation of the tannin material in apple tissue, but although injections were made with various substances to try and produce this effect, e.g. acids of varying strength, etc., these attempts were unsuccessful, and almost invariably resulted in the formation of the red spots and patches except in the case of strong tannic acid which produced a hole surrounded by a pale margin.

A certain species of Jassid bug found feeding on horse chestnut and producing white spots thereon, was transferred to apple on which it produced similar white spots; apparently these cells were not dead or else, as suggested above, some substance was injected which prevented the formation of the red pigment. Lefroy and Horne (6), in their paper upon the effects produced on plants by sucking insects, put forward the theory that these white patches consist of cells filled with air. White spots are characteristic of the feeding of Jassid bugs, each plant damaged by them responding in a similar manner, at any rate in those cases of which the writer has personal knowledge, i.e. apple, pear, chestnut, and potato.

An interesting parallel case to that of the Capsids is found in the apple-feeding aphids, *Aphis pomi*, and *Aphis sorbi*; one of these has little effect upon the foliage while the other (*Aphis sorbi*) causes curling of the leaves and the formation of a very bright pink pigment which is visible on the trees from a considerable distance, and which gives to the Aphis its name of Rosy Apple Aphis. Sections through this rosy material present an appearance exactly similar to that of sections through tissue damaged by *P. rugicollis*, i.e. dead cells filled with a granular material the only difference being in the colour of the pigment.

Experiments were then made with another species of Capsid known to be harmful to other plants, this was *Lygus pabulinus*, already mentioned in connection with the experiments upon potato; it is a very common insect and does considerable damage to the foliage of currant bushes, and produces the "shot hole" effect on potato plants. A number of these bugs were taken at a very young stage and "sleeved" upon apple trees, they took very rapidly to this new food and produced on apple and willow injury absolutely identical with that produced by *P. rugicollis*; the change of food plant seemed to have no ill effect on the bugs, and they mostly became adults, very few dying.

Extracts were made of the salivary glands of this insect and injected into apple and willow, causing the same effect as that produced by the extract of *Plesiocoris rugicollis*. It seems fairly certain that a Capsid that produces damage to one plant produces damage to every plant upon which it feeds, although this damage varies slightly according to the reaction of the plant juices to the saliva. No case was found by the writer of a Capsid that was harmful to one plant being harmless to another, and conversely the harmless apple bugs, when induced to feed upon willow, were harmless to that also.

Lygus pabulinus was found feeding upon many different plants and trees, as shown in the following list; the effect produced in each case is given.

Red Currant. Reddish white patches and puckerings of leaves. Fruit untouched.
Black Currant. Whitish patches on leaves. Fruit untouched.
Pear. Black spotting of fruit and leaves.
Apple. Red spots and patches.
Plum. Red spots and patches.
Gooseberry. Reddish white patches on leaves. Fruit untouched.
Bindweed. Clear patches of dead cells. Similar to damage to willow.
Dock. Red spots.
Artichoke. Whitish patches with crinkling.
Potato. Brown spots. "Shot Hole" effect.
Willow. Clear patches of dead cells. Compare Bindweed.

This list would apply equally well to the effects produced by *P. rugicollis*.

In all the above instances *L. pabulinus* was found feeding under natural conditions except in the case of the apple where they were "sleeved" on the tree. A number of young specimens of *L. pabulinus* were placed on small apple trees growing near some currant bushes without any measures being taken to prevent their escape; they remained upon the apple trees several days, causing a certain amount of damage, and then migrated to the currant bushes. It seems probable that if these specimens had been newly hatched they would have stayed upon the apple trees as it is quite easy to rear them under controlled conditions upon apple from early stages to adults.

An American worker, C. R. Crosby (7), records two species of Capsids, *Heterocordylus malinus* and *Lygidea mendax*, as living upon apples in America, and describes and figures injury exactly similar to that produced by *Plesiocoris rugicollis* and *Lygus pabulinus*, the two species more particularly dealt with in this paper.

An interesting point arises as to why *P. rugicollis* should have changed its food plant from willow and alder to apple, and if this species could do so why should not *L. pabulinus* do the same? It will be seen from the table of food plants that it has already a varied diet, it can also be easily reared upon apple as shown, so that it would not be altogether surprising if another pest were added to the already very long list of those attacking and injuring apple trees.

An attempt was made to find out the nature (acidity or alkalinity) of the salivary juices of various harmless and harmful bugs. Some specimens of *L. pabulinus* and *P. rugicollis* and *Psallus ambiguus* were starved for 24 hours and then introduced into a petri dish containing red and blue litmus paper soaked in sugar solution. The bugs would not as a rule insert their stylets more than once; the result of the insertion was to leave a brown spot on both red and blue litmus paper.

SUMMARY.

There are several species of Capsid bugs which normally feed on the leaves and fruit of apple trees but only one causes any damage, i.e. *Plesiocoris rugicollis*. This species produces the death of the tissue surrounding each puncture in the leaves made in feeding and on the fruit produces great distortion and "russeting."

There are three possible explanations of this damage:

(1) A purely mechanical injury produced by the insect's stylets in process of sucking.

(2) The possibility of the bug acting as a "carrier" of bacteria and by injecting these into the plant along with the saliva so sets up a pathological state.

(3) The injection of some secretion from the salivary glands which has a violently toxic effect on the plant tissue.

It was found impossible to reproduce by mechanical means the injury resulting from the feeding of *P. rugicollis*, also the fact that the other species of Capsid bug feed in a similar manner and produce no injury militates strongly against the theory of mechanical injury only.

As regards the second theory, no bacteria could be discovered in microtome sections of either damaged plant tissue or the salivary glands of the bug, and all attempts to reproduce the damage by means of bacteria failed.

The third theory was proved to be the correct explanation by several experiments and observations.

Experiments were made to try and reproduce the bug injury with various dilute poisons; in most cases a very similar appearance was produced in the foliage, but the attempts were unsuccessful in the fruit itself with the exception of the very great retarding effect in the growth of the fruit, which is one of the results of the bug injury.

By feeding the bugs on slices of potato instead of apple the same

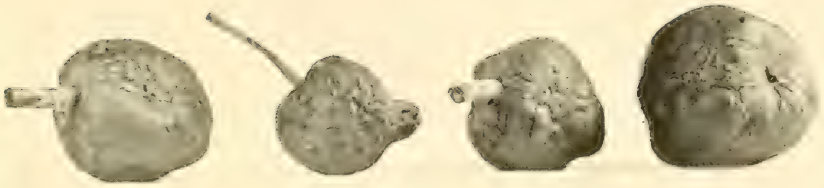

Fig. 1.

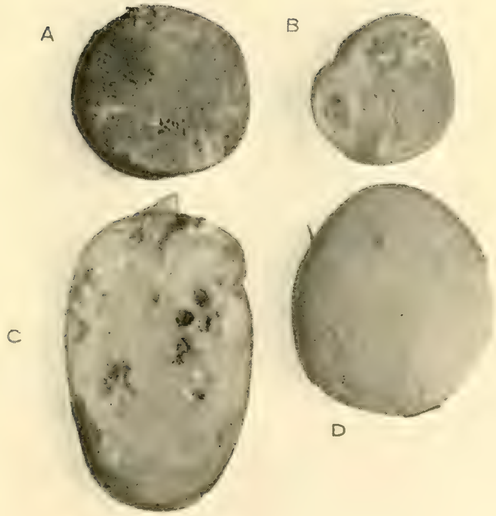

Fig. 2.

effect was produced, but on a magnified scale. The salivary glands of *P. rugicollis* and of *Lygus pabulinus*, a bug harmful to potato foliage, when placed on a freshly cut slice of potato in a petri dish, produced a violent reaction which killed much of the tissue surrounding the glands. The same experiment was carried out with the glands of one of the harmless apple-feeding bugs *Psallus ambiguus*, these had no effect whatever on the potato. When the salivary glands of *P. rugicollis* were pricked into apple buds, the shoots were killed within 24 hours. The salivary glands of *P. ambiguus* when similarly treated had no effect. Observations were made showing the rate of exudation of sap from the bug's puncture in the potato and these are given for *P. rugicollis* and *Lygus pabulinus*. A list of common plants and fruit trees with their various reactions to the feeding of harmful bugs is also given.

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EXPLANATION OF PLATE III

Fig. 1. Photograph of four apples, showing the typical damage produced by *Plesiocoris rugicollis*. Note the "scab" effect.

Fig. 2. Photograph of four slices of potato. A, B damaged by *L. pabulinus*, C by *P. rugicollis* and D fed upon by *Psallus ambiguus*, but undamaged. In A, B, note the large punctures surrounded by dead and blackened tissue.

EXPLANATION OF LETTERING.

An. Antenna. *C.R.* Collapsed Reservoir. *Lbr.* Labrum. *Lb.* Labium. *Md.* Mandibles. *Mdl.* Mandibular lever. *Md.C.* Cavity of the mandibles. *Md.H.* Hooks of Mandibles. *Mx.St.* Maxillary Stylets. *R.* Reservoir. *Sd.* Salivary duct. *Sg.* Salivary gland.

SPHAERONEMA SP. (MOULDY ROT OF THE TAPPED SURFACE).

By A. R. SANDERSON, F.L.S. and H. SUTCLIFFE, A.R.C.S.

(*Mycologists to the Rubber Growers' Association,*
Federated Malay States.)

(With 4 Plates.)

The treatment to which the rubber tree (*Hevea brasiliensis*) is subjected in order to obtain the latex, viz. excision of bark and the major portion of the cortex in the form of thin shavings at frequent and regular intervals (this constitutes the operation known as "tapping"), leaving only a thin cover of the inner cortex overlying the cambium, is such that there is little cause for wonder when one learns that the exposed tissue is attacked by fungoid pests, some of which are capable of establishing themselves as parasites in the cortical tissue. Some indeed go further than this and pass through to the wood elements beneath and becoming firmly established there, spread up or down in a vertical direction, killing the cambium and the cortical tissues outside.

One of the most dangerous of these parasites, since it destroys the cortical tissue and thus ruins the tree so far as the production of revenue is concerned, is a species of *Sphaeronema* which is the responsible agent in causing the rotting or destruction of the tapped surface, i.e. this fungus utterly destroys the thin skin of cortex remaining after tapping, hence delaying the renewal, and in fact making it almost or quite impossible for tapping to be carried on over that section again. Normally a tapped surface can be tapped over again in from 5–6 years or even sooner, as by that time the regenerated cortex is sufficiently mature to yield an amount of latex which is remunerative.

In the *Agricultural Bulletin of the Federated Malay States*, Vol. VI, No. 1, October 1917, Messrs Belgrave and de la Mare Norris writing on Bark Cankers and their treatment, describe a bark canker as "Mouldy Rot of recently Tapped Surface." Though stating that inoculation experiments indicate *Sphaeronema* as the causal fungus they apparently had not definitely determined the point.

The disease was originally confused with another well-known and wide-spread disease of the tapped surface, viz. Black Thread or Black Line Canker the causal fungus of which is a species of *Phytophthora*, Mouldy Rot being considered a virulent form of this.

Further investigation however showed that *Phytophthora* sp. was never present in tissues affected by Mouldy Rot, species of *Cephalosporium, Fusarum, Sphaeronema* are constantly present and occasionally several other saprophytic fungi and bacteria are to be found in the tissues.

The writers commenced their investigations of this disease in December 1918 and in March 1919 issued a preliminary note on the subject (First Malayan Report, 1919, Rubber Growers' Association).

The fact that a species of *Sphaeronema* had already been suggested as the causal fungus, determined us in working first on this fungus, especially as the other fungi present in the diseased tissue are common and well known saprophytes. Attempts to isolate the *Sphaeronema* by means of pycnidiospores in the usual ways all failed, chiefly owing to the fact that they are exuded in a sticky mass, almost impossible to separate into individuals, and foreign matter, spores etc. is held tenaciously. These spore masses refused to separate in liquefied nutrient agar, and frequently were killed at the temperature necessary to keep the agar in a liquid condition.

We then tried to isolate the fungus by picking out resting spores under the microscope, but the results were not encouraging. Finally we decided to try the mycelium fairly deep in the tissues and this gave the best results in the shortest time. Experiments with inoculations of *Cephalosporium* and *Fusarium* on stripped surfaces gave always negative results.

ISOLATION OF THE FUNGUS.

Portions of old dry bark which had been affected with mouldy rot were used as the starting point in investigating this disease. A portion of bark 6 inches square was removed from a healthy tree and the underlying fresh tissue exposed. Inoculation was effected by scraping the old infected bark, mixing the scrapings with distilled water and applying with a soft brush.

At the same time the inner surface of the bark removed was inoculated similarly, cut into four portions 3 inches × 3 inches and kept under observation in covered glass dishes.

In 48 hours all the inoculated surfaces had become discoloured, turning a dirty brown, and by the end of the fifth day the cells of the outer surfaces in all cases had been completely killed. Species of *Cephalosporium*, *Fusarium*, etc., were gradually covering the whole with white mycelium, and bacteria were completing the work of destruction. Portions of infected bark and wood were examined microscopically after 48 hours and again after six days. The mycelium had in places penetrated to a depth of $\frac{1}{10}$–$\frac{1}{8}$ inch, apparently penetrating most deeply along the medullary rays and then spreading laterally more slowly. Even in cells almost filled with mycelium, the nucleus in some cases was still present and apparently unaffected after six days, but in most cases, of the cells attacked, the contents had disintegrated or entirely disappeared. In the bark, cells containing tannin were also attacked. A few characteristic fruits (pycnidia) had developed by the end of the fifth day and quite a large number in six days, the surface where these appeared having turned quite black.

A mass of spores just emerging from the apex of a pycnidium was carefully removed on sterilised needles, the operation being conducted with the aid of a high power lens; the moulds present, *Cephalosporium*, *Fusarium*, etc., were as far as possible excluded and inoculations made on agar and on fresh bark sterilised outside with picro-formal, and then placed straight from the tree into sterilised tubes.

The bark showed the typical brown discolouration round the point of inoculation at the end of 24 hours.

One of these pieces of bark after six days growth was sterilised in 1/500 corrosive sublimate solution, then washed with freshly boiled distilled water, and finally the upper (previously infected surface) being the original inner surface of the bark shaved off with a freshly sterilised chisel. A second shaving was then taken from the surface newly exposed, this presumably contained active pure mycelium, and in fact such proved to be the case, as on being brought into contact with clean bark fresh from the tree, the characteristic colouring was apparent in 18 hours, while the controls remain unaltered. In every case of successful inoculations, the attack spread with quite remarkable rapidity.

CULTURES.

Cultures were set up from spores removed from pycnidia produced on bark as above, on Prune agar, 2 per cent. virol agar, Quaker oat agar, agar made with infusion of rubber tree bark, and in every case pycnidia were produced in abundance in from five to nine days. Similar cultures on sterilised wood produced an abundance of pycnidia and also resting spores in from 10–15 days. Cultures on 2 per cent. cane sugar agar gave very good results. The growth on dolichos agar and on bean agar was much slower than on those previously mentioned, pycnidia however were produced even on these in about 20 days and a fair number of resting spores in the same time. In every case of inoculation of freshly exposed surfaces of bark or wood, infection was set up, and the disease rapidly spread over the entire surface exposed, more particularly when an excess of moisture was present.

In six cases portions of bark about six inches square were removed from the tree, and the exposed underlying surface inoculated with spores from pycnidia in water. When a considerable number of pycnidia had been produced on all these surfaces and they all showed the characteristic appearance of mouldy rot, jodelite was applied, and the next day a fresh portion of bark removed below, but in continuation with the first surface exposed. In every case the disease appeared on the fresh surface at the end of two days. Discolouration was apparent as a continuation from the previously affected part, the disease having spread downwards in the wood and innermost layers of bark. A similar experiment was carried out but fresh surfaces exposed laterally. The disease again spread to the freshly exposed surfaces.

Many of the cultures on artificial media produced considerable numbers of resting spores embedded in the media well below the surface. These large resting spores are produced in from 8–10 days after inoculation, and, being thick walled can withstand considerable desiccation without losing the power to germinate. Some infected material which could not be dealt with at once, was put aside in a desiccator so as to keep it as clean as possible, i.e. to prevent spores of various saprophytic fungi which are almost invariably present in the air from lodging on it. Six weeks later portions of the tissue were taken and infections obtained from resting spores, on stripped surfaces, thus proving that the extreme desiccation to which the spores had been subjected had not succeeded in killing them. They are produced in abundance on the infected surface in dry weather, taking the place of the pycnidia. The third type of spores which so far we have only found in cultures in the laboratory, is very similar in size to the pycnidiospore and is cut off directly from the mycelium. Examination of infected cortical tissue in which the disease had been present 8–10 days showed that large numbers of globules of an oily or fatty nature were present. These varied much in size and were fairly evenly distributed throughout the tissue, which had been killed by the fungus.

Cortical tissue which had been affected for a considerable time contained these globules sometimes in great abundance, some of the cells being full of them. No trace of these could be seen in the cultures on artificial media, they are not present either in recently infected, or normal healthy cortex. Tissue which had been killed and partially destroyed by the *Sphaeronema* formed then a suitable nidus for bacteria which were present in abundance. One case of inoculation on a stripped surface which was kept under observation proved very interesting.

The surface was inoculated 27/11/18 and six days later pycnidia appeared. In the meantime the mycelium had spread over the entire surface exposed (about 24 square inches).

Cultures were made from pycnidiospores and the surface was then left, i.e. no fungicide was applied.

By 28/12/18, approximately a month later, healing from the edges had made fair progress and a month later still the wound appeared to be in a fair way to recovery.

More cortex was removed 2/2/19 both above and below but in continuation with the part previously exposed, and in less than four days there was the usual appearance on these stripped surfaces showing that the disease was spreading. In eight days pycnidia appeared on these newly exposed surfaces and examination of portions of wood in sections from the original surface showed that the mycelium had penetrated $\frac{1}{8}''$ and was then spreading slowly in a vertical direction.

Other cases similar to the above inoculated 5/12/18, and treated with an antiseptic cover, but in which no further surfaces were exposed, have now almost completely healed over. The cortex shows no signs of disease (9/1/20) and there is every appearance of complete recovery. Regeneration from the sides will however give a very uneven surface to tap over.

During wet weather pycnidia are produced in abundance on the affected surfaces while resting spores are not at all common. In some cases where the disease proved most difficult to keep in check during a prolonged spell of dry weather, no pycnidia were produced, but immense numbers of resting spores were formed on the surface and some were also found embedded in the tissue several cells deep. Under those conditions it is probable that the resting spores provide an even surer means of distribution than the pycnidiospores and these as well as those in the tissue are equally dangerous so long as tapping is continued, the knife then being the chief agent in their distribution from tree to tree.

The pycnidiospores are quickly killed by desiccation but the resting spores can withstand this for quite a long time.

DESCRIPTION OF THE FUNGUS.

The causative fungus is a species of *Sphaeronema* which belongs to the group *Fungi Imperfecti*.

The mycelium is dark coloured—brownish—the filaments are formed of cells varying much in length compared with the width, much branched, and under suitable conditions as regards moisture, etc. grows rapidly at the expense of the host. Normally the fruiting body, a pycnidium, is produced by the end of the fifth or sixth day after inoculation. These were produced in abundance in cultures in the laboratory in about the same period as on the trees attacked.

The pycnidium is quite characteristic and should always be looked for in supposed cases of "Mouldy Rot." A pocket lens of powers × 10 diameters shows it up quite well. When mature it is a black, flask-shaped body ·12 mm.–·24 mm. wide at the base and ·24 mm.–·9 mm. long including the long narrow neck which is ·02 mm.–·024 mm. wide. The long neck has a distinctly striated appearance due to the presence of thicker portions in the form of strands. At the apex the strands split apart somewhat from the connective tissue (see Pl. IV, figs. *a* and *b*) facilitating the discharge of masses of pycnidiospores.

The pycnidia arise directly from masses of the dark coloured mycelium, which with the black pycnidia give the infected surface a black appearance; as the attack progresses this effect is accentuated. Pycnidia are, under favourable conditions produced in immense numbers, many hundreds being crowded together in quite a small area. The pycnidiospores are produced in the base of the pycnidium, and in a sticky matrix are gradually forced up and out of the neck, adhering when freshly exposed as a white, more or less globular, sticky mass, which rapidly turns brown when dried.

Eventually the mass is pushed over the side and remains sticking to the outside of the neck, being followed in a very short period—24 hours or more—by a second mass. The masses of pycnidiospores are very quickly affected by desiccation. By the time the mass has turned dark brown, it may be quite a short time after expulsion from the pycnidia, they have lost all power of germination, hence a dry season helps greatly in controlling the disease while a wet one makes it more difficult. This has however proved not always to be the case, as in some cases immense numbers of resting spores are produced when pycnidia are altogether absent during a dry period. The individual pycnidiospores 2·5 microns × 4 microns are slightly attenuated and rounded at the ends. When fresh they germinate almost immediately on a suitable medium, e.g. a fresh surface exposed by tapping. Besides these, two other kinds of spores are produced, one being a large, almost spherical, thick walled resting spore 10–20 microns in diameter (the great majority are 10–14 microns in diameter) produced at the ends of short lateral branches, especially on the mycelium at or near the surface (see Pl. IV, fig. *c*). Cases have been observed where these spores were produced on the mycelium embedded in the tissue several cells deep, and in the particular cases observed pycnidia were scanty or entirely absent (see Pl. V, fig. *a*).

From the experiments and field observations it would appear that with a high percentage of humidity pycnidia will usually be produced very quickly in large numbers, while under dry weather conditions the resting spores are produced sometimes in almost equal abundance. It follows of course that weather conditions cannot be relied on as an aid in checking or eradicating the disease.

Deep tapping undoubtedly aids in the thorough establishing of the fungus in the tissues since under those conditions penetration to the wood is quickly effected.

Much wounding during tapping also aids in a similar way.

SYMPTOMS OF ATTACK.

A freshly exposed surface of *Hevea* attacked by *Sphaeronema* turns darker in colour than normal in quite a short time (24 hours). In three days the infected surface rots, and various species of saprophytic fungi make their appearance on the dead tissue, the presence of these being indicated by the tell-tale more or less complete cover of white mycelium. This appearance is most noticeable one to two inches above the cut. Portions of the tapped cortex sink in, forming depressed patches of various sizes, which may in a bad case extend the whole length of the cut. The affected portion frequently turns quite black. Later, in neglected cases, the fungus penetrates the wood $\frac{1}{12}''$–$\frac{1}{8}''$, spreading vertically up and down the wood fibres.

The less serious cases where only small portions of the cortex become depressed resemble Black Line Canker, but usually pycnidia may be found, sometimes in considerable numbers.

The damage caused by this disease when neglected is probably greater than that due to any other bark disease of *Hevea*. The disease continues as long as tapping is continued and is easily spread from tree to tree by the knife.

Cortex destroyed by *Sphaeronema* is frequented by small Diptera and beetles both of which are liable to spread the disease especially by carrying the pycnidiospores which adhere to the legs and bodies.

Since the fungus quickly produces spores (5–6 days) once a tree is attacked and the initial attack overlooked, the spread of the disease is usually very rapid and whole tasks of 300–400 trees may be affected in the course of a week or fortnight.

The rapidity of spread and the short time in which it kills the tissues make this a most dangerous disease. A week may see the number of infections increased by hundreds.

The loss sustained by an estate affected by Mouldy Rot, unless efforts are at once made to obtain control and eradicate the pest, may be very great, as once it becomes fairly widespread tapping must be stopped for periods varying from 2–6 months and this may have to be repeated after reopening if the disease shows signs of reappearing. The distribution of remaining cortex after tapping also is bound to be serious if it continues for any length of time since a shortage of bark means loss of revenue.

When reopening trees after a period of rest due to Mouldy Rot the new cut if in the same section should be 4 inches below the old one; it is better to open up a new section and keep a sharp watch for any new infection which should be dealt with vigorously.

Two other species of *Sphaeronema* have been seen frequently by the writers growing as saprophytes on dead *Hevea* timber; one often appears on the cut surfaces of fresh timber during felling. These are always accompanied by hosts of small diptera which apparently find the sticky masses of pycnidiospores an attraction. Both these species produce fruit (pycnidia) viz. quickly, one of them usually in about three days or even less.

We are indebted to the Rubber Growers' Association for permission to publish the results of this work carried out on their behalf.

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First Malayan Report 1919. Rubber Growers' Association, *Kuala Lumpur*, F. M. S., March, 1919.

Third Malayan Report for 1919. Rubber Growers' Association, *Kuala Lumpur*, F. M. S., December, 1919.

DESCRIPTION OF PLATES

PLATE IV.

Fig. (*a*) Pycnidium and mycelium of *Sphaeronema* sp. Note the mass of spores at the apex of the pycnidium. × about 60.

Fig. (*b*) Apex of pycnidium showing spores and strands. × about 190.

Fig. (*c*) Resting spores of *Sphaeronema* sp. These occurred commonly during a prolonged period of dry weather when no pycnidia were produced. × about 130.

Fig. (*d*) Section of infected tissue showing pycnidia and resting spores on the outer surface. × about 32.

PLATE V.

Fig. (*a*) Section of infected cortex showing resting spores formed within the tissue. × about 200.

Fig. (*b*) Section of wood showing the mycelium of the fungus in the cells. Nuclei are still present in some cases, the rest of the cell contents being destroyed. × about 225.

Fig. (*c*) Resting spores produced on artificial medium (nutrient agar jelly) after 8 days. × about 100.

Fig. (*d*) Mycelium in cells of diseased cortex. × about 200.

PLATE VI.

Fig. 1. Recently tapped surface (A) attacked by the disease.

The white felt-like masses of mycelium of saprophytic fungi, chiefly Cephalosporium, are irregularly distributed over the decayed surface. The real cause of the disease is more deeply seated and is spreading downwards keeping pace with the tapping. The cortex B–C had been treated with an antiseptic tar mixture several times. Portions of the exposed wood so treated (D) some considerable time after treatment showed irregular white patches. These were due to a granular deposit the result of some chemical action, of the disinfectant cover on the tissues.

Figs. 2 and 3 illustrate the effect of mouldy rot on a freshly stripped surface. Two portions of cortex were stripped at the same time.

(*a*) Was inoculated with spores of *Sphaeronema* in distilled water, the spores being placed on the surface with a soft brush.

(*b*) Was not inoculated (control).

Fig. 2 shows the appearance 24 hours after inoculation.

Fig. 3 shows the appearance six days after inoculation.

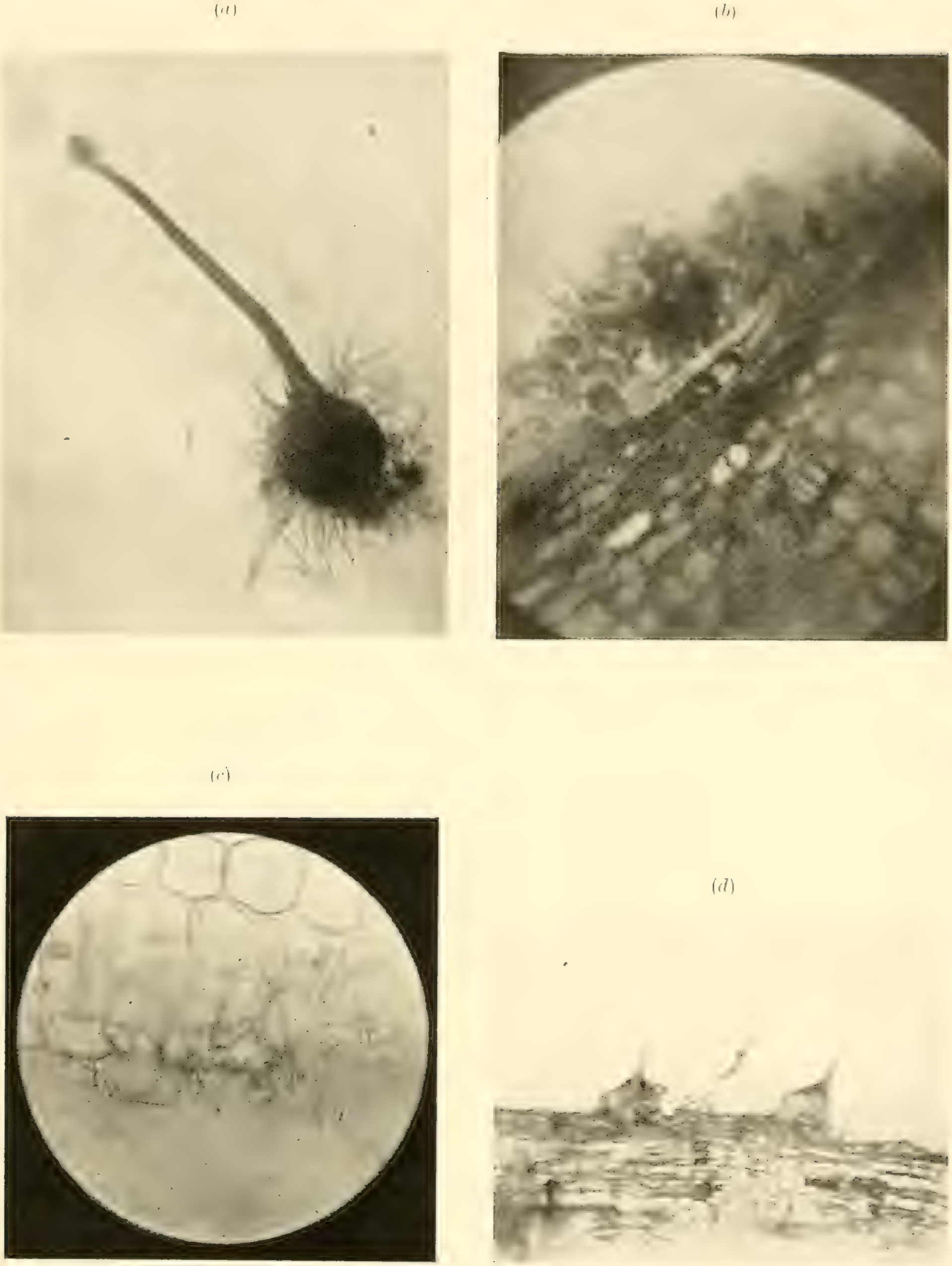
Within six days the *Sphaeronema* had produced pycnidia. It will be noticed that on the infected surface, the cortex is utterly destroyed down to the wood. Saprophytic fungi are present on the decayed tissue. × about $\frac{1}{6}$.

PLATE VII.

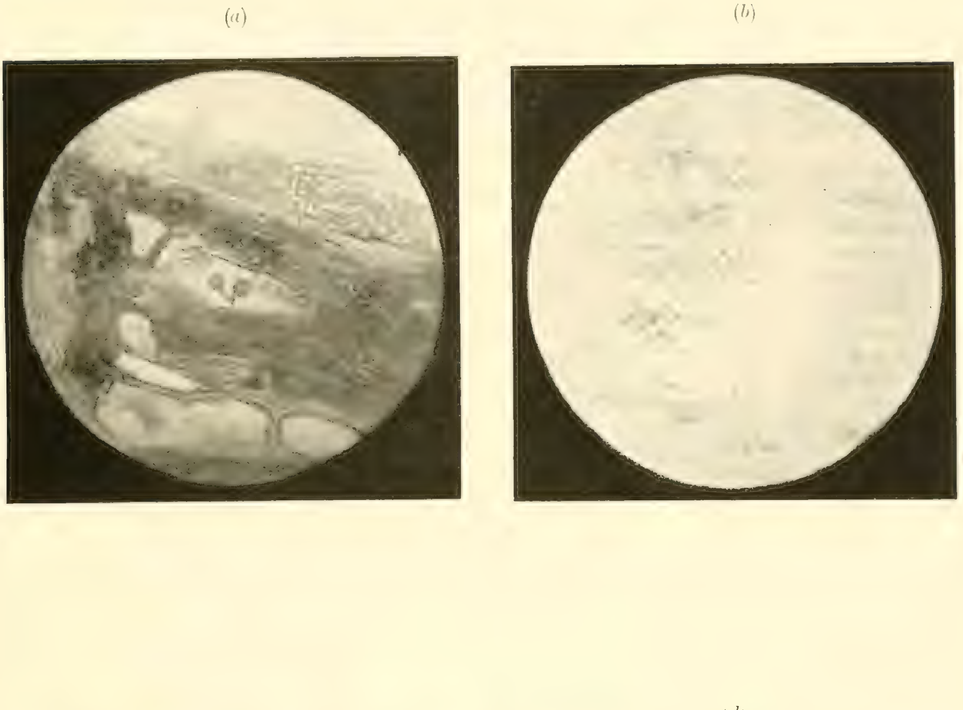
Fig. 1. Tapped cortex of *Hevea* attacked by mouldy rot. The disease which started at A followed the tapping down to B and is still continuing.

Fig. 2. Extension of the disease to new cuts. The disease had almost completely destroyed tne tapped surface A–B (over 3 feet). A new cut was then opened at C on a new portion, infection quickly followed because the disease was still carrying on all round in other trees. The new infection is as previously keeping pace with the tapping (C–D).

Note the large open wounds on the surface A–B, and C–D will show a repetition of this. When the new cut started at C is finished, there will be no tappable cortex left below 4 ft. from the ground.



Sphaeronema sp.



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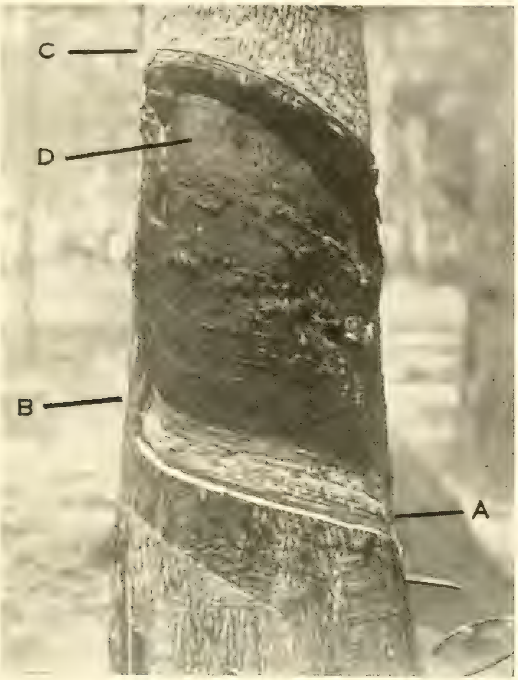

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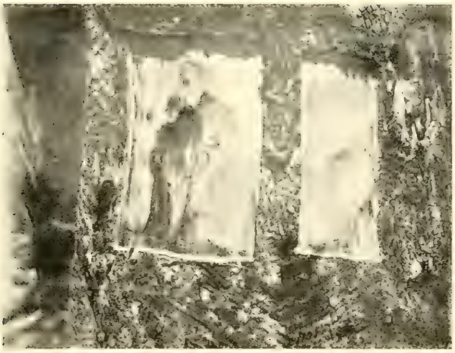


Fig. 2.

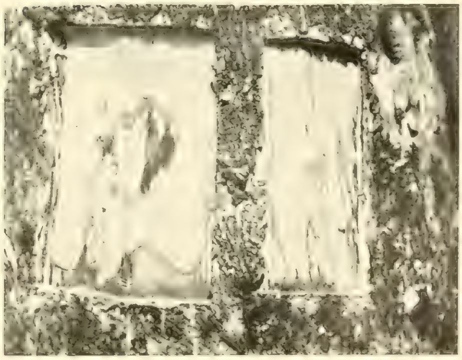
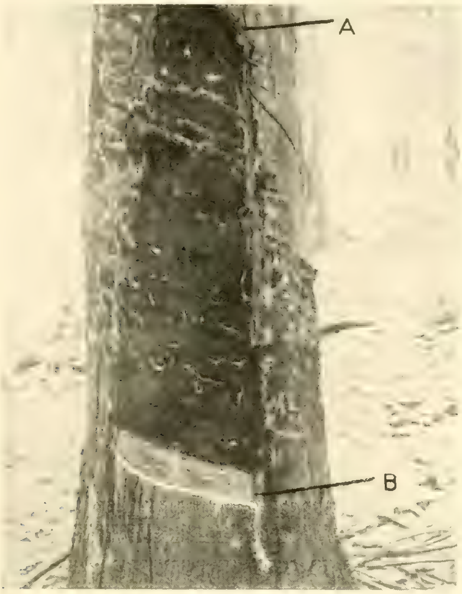


Fig. 3.

Sphaeronema sp.



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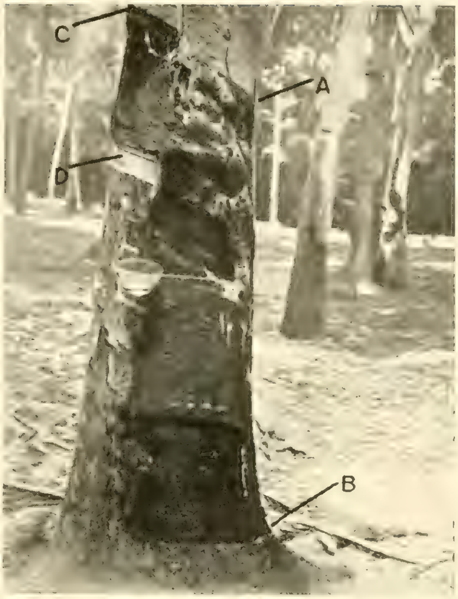

Fig. 2.

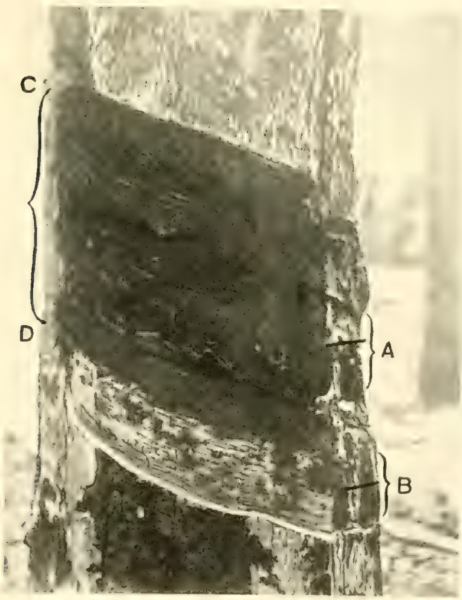

Fig. 3.

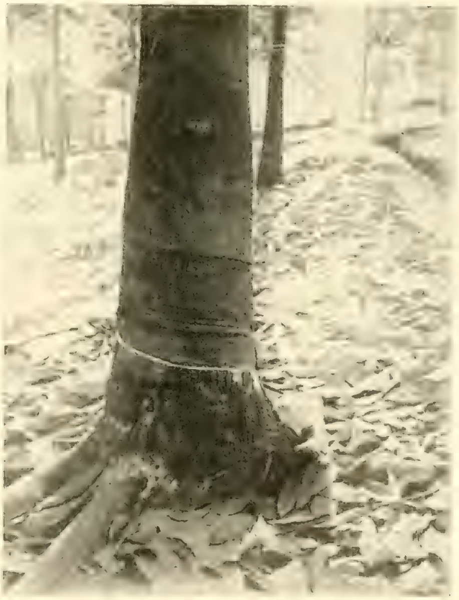

Fig. 4.

Sphaeronema sp.

Fig. 3. In this specimen 20 inches of bark have been removed on the new cut. Fifteen inches of tapped surface is almost completely destroyed. The lowest five inches (B) shows the disease is still present in a virulent form.

Note the portion (A) where open wounds extend across the tapped surface.

The portion C–D had been treated (too late) several times with an antiseptic cover.

The fungus is present in the wood and has already passed below the present cut, hence the disease will persist so long as tapping continues. The tree figured was one similar to that in fig. 2. The whole of one tapped surface (over 3 ft.) was completely ruined, and the second cut, which showed infection almost immediately after opening, is merely a repetition of what occurred on the previously tapped surface.

Fig. 4. Photograph showing tapped surface and tapping cut of a normal 15 year old *Hevea* tree unaffected by disease.

THE HABITS OF THE GLASSHOUSE TOMATO MOTH, *HADENA (POLIA) OLERACEA*, AND ITS CONTROL.

By Ll. LLOYD, D.Sc.

(*Entomologist at the Experimental and Research Station, Cheshunt.*)

(With 3 Plates and 4 diagrams.)

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1. INTRODUCTION.

HADENA OLERACEA appears to have been first noticed as a pest of tomatoes grown under glass about 30 years ago at Enfield Highway. Since that time it has spread throughout the whole of the Lea Valley, the most important of the tomato-growing centres in England. In recent years it has become very serious at Worthing and at Harpenden, and it has also been noticed in Denmark, where it has not yet become a serious pest.

The destruction of the foliage by the larvae is considered to be of less importance than their habit of feeding on the fruits, and biting into the stems of the plants. It is no uncommon thing to find three or four fruits on a truss thus destroyed by a single larva in a night. One grower had three tons of fruit destroyed by this means out of a total crop of 40 tons in the season. Another, who grows an acre of tomatoes, estimates that the pest cost him £150 in the present year, in spite of the fact that he partially controlled it by spraying. In a recent year the damage in the Lea Valley alone was estimated at £30,000, but when the cost of picking off the larvae by hand is added to this it is certainly an underestimate. In some cases the whole staff of a nursery have had to be occupied on this work, to the neglect of other duties, in order to bring the pest within bounds.

The Experimental Committee of the Lea Valley Tomato Growers Association therefore approached the Director of the Rothamsted Experimental Station with a view to the provision of an Entomologist to investigate the habits of the moth and to indicate means of control. Experiments were carried out in a large trade nursery, and laboratory work was done at the Cheshunt Experimental and Research Station. The thanks of the entomologist are due to the President of the Association, Mr H. O. Larsen, J.P., for his unfailing assistance in the conduct of the experiments in his nursery, given often at considerable inconvenience; to Mr A. Bacot of the Lister Institute of Preventive Medicine, who has helped greatly with his wide knowledge of the habits of the British Lepidoptera; also to Dr A. D. Imms, Chief Entomologist of the Rothamsted Experimental Station, who has been frequently consulted.

This report embodies the work done from the middle of April to the end of September.

2. CHARACTERS, LIFE HISTORY, AND HABITS.

The species is common and generally distributed throughout the British Isles to the Shetlands, the greater part of Europe, and also occurs in Asia Minor (Meyrick). The moth normally flies in June and July, with sometimes a partial second brood in the autumn. The larvae feed on a wide variety of low plants, and on certain shrubs and trees. In the neighbourhood of the nurseries they have been observed out of doors on *Polygonum*, *Chenopodium*, *Rumex* and *Brassica*, and on one occasion on tomato. The eggs were found on nine occasions on *Chenopodium*, but were not observed on any other plants.

(i) The Moth.

The moth measures 1½ to 1¾ inches (35–40 mm.) across the wings. The fore wings are purplish brown, sometimes brownish drab, with a few scattered white scales. The first and second lines across the wings are very faint and there is a fine well-marked white subterminal line provided with two sharp median tooth-like projections. The orbicular and reniform stigmata are usually whitish edged, the former bearing a yellowish spot in its centre. Hind wings greyish, usually with a fuscous discal crescent and a posterior clouding or suffusion. There are no sexual differences in the markings. The general appearance of the insect may be gathered by a reference to South's *Moths of the British Isles*, Vol. I, Pl. 120.

The females largely outnumber the males. From among 152 moths bred from pupae in the laboratory, 103 (68 per cent.) were females and 49 (32 per cent.) were males: out of 1230 trapped in the greenhouses 872 (71 per cent.) were female and 358 (29 per cent.) male. The sexes were distinguished by squeezing out the genitalia after death. The proportion of females is therefore about 70 per cent., and as in cages where the moths were kept in their natural proportions practically all the eggs were fertile, it must be assumed that one male can fertilise several females.

The moths in the greenhouses hide under clods of earth or amongst the mulch, sometimes in dark places under the gutter-boards and occasionally on the undersides of the leaves. They are rarely seen by day except when they are disturbed by watering. They commence to fly at dusk and may then be seen beating along the glass and endeavouring to escape. Sometimes they work along cracks where fresh air flows into the houses and attempt to force their way through. This attempted and partially successful emigration of the moths is probably due to a dislike for the atmosphere of the houses, as other species which pass in by accident behave in the same way. These activities draw a large proportion of them to that part of a block of glasshouses which is most strongly lit at dusk, and thus an end house of a block, or the ends of all the houses along one side, become more heavily infested with caterpillars than the other parts. These heavily infested parts, in the cases which have been investigated, have always been found to be towards the south-west. Additional evidence of this is afforded by the following facts. In systematic trapping by means of 36 traps, evenly distributed through a block of 12 houses over a long period, 1444 moths were caught in the 12 traps along the southern side upon which the light at sunset fell (the west end being shaded by a grove of trees) while only 956 were taken in the 12 traps on the northern side, which was darker at dusk. In the trap in the south-west corner of the block 194 moths were caught, a number which is more than double the average catch (80) of all the traps exposed during the same period.

The moth commences to lay eggs on the second or third day after emergence from the pupa. Sometimes the eggs are laid singly, but usually they are placed in large batches. The moth first lays a well-ordered layer which is distinctly arranged in rows of four. On these a second smaller layer is often placed, and sometimes a third layer is added, when the patch of eggs appears to be a disordered heap. The number of eggs laid in a batch varied up to a maximum of 325, the average number in a hundred batches being about 66. They are almost invariably placed on the lower surfaces of the leaves. On only one occasion has a batch been found on the upper surface.

The moth is long lived, especially if food is obtainable, and its egg production is greatly increased by feeding. Both sexes feed eagerly on the juice of broken ripe tomato fruit, and as these are carelessly left to rot in many nurseries this food is of easy access to them. Even without food however the moth is a prolific one, as the following experiments show.

Table 1. *Showing the effect of supplying broken ripe tomato as food to the moths in captivity.*

	Moths fed	Moths not fed
Number of moths employed	22	28
Number of males	5	9
Average life	21 days (12 to 28)	10 days (5 to 15)
Number of females	17	19
Average life	19 days (9 to 29)	11 days (6 to 16)
Total eggs laid	190 batches	91 batches
Average batches per female...	11·2 batches	5·3 batches
Average eggs per batch ...	78	55
Average total eggs per female	872	263

Moths were enclosed in two cages constructed of a frame-work of wood, with three sides and the roof of muslin, and one side of glass; the dimensions being about 18 in. × 18 in. × 2 ft. high. Tomato or other plants in pots were placed in these. In one cage a broken ripe tomato was supplied, and in the other a dish of water but no food. The moths were placed in the cages on the day of their emergence, and the length of life was found by noting the dates of their deaths. The number of batches of eggs laid was counted, and counts of the eggs were made from 50 batches removed at random from each cage. The results are shown in Table I.

A fed female moth on the average survived a month and produced nearly 900 eggs. Under more natural conditions the number is probably greater. Access to food doubled the average life of the moths and the average number of batches of eggs laid. It increased by 33 per cent. the average number of eggs in a batch, and a fed female produced more than three times the number of eggs laid by an unfed one. A repetition of the experiment gave similar results: six fed female moths, with an average life of 14 days, laid 66 batches of eggs, and seven unfed females, with an average life of six days, laid 13 batches.

Table II. *A study of the selection of the food plant by the moth.*

Series	I	II	III	IV	V
Total No. of batches of eggs ...	68	41	74	78	71
Plant		Percentages of batches			
Tomato	4·4	25	38	18·2	31
Chenopodium album (White goosefoot)	38·2	37	62	—	69
Urtica dioica (Stinging nettle)	1·5	—	—	19·2	—
Solanum dulcamara (Bittersweet) ...	8·5	13	—	15·4	—
Senecio vulgaris (Groundsel)	4·4	—	—	15·4	—
Convolvulus arvensis (Bindweed) ...	4·4	—	—	—	—
Rumex acetosella (Dock)	4·4	—	—	11·5	—
Taraxacum officinalis (Dandelion) ...	5·9	—	—	—	—
Plantago major (Plantain)	10·2	13	—	1·3	—
Lamium purpureum (Dead nettle) ...	0	—	—	20·5	—
Polygonum aviculare (Knotgrass) ...	5·9	—	—	0	—
Lettuce	8·8	14	—	—	—
Cabbage	1·5	—	—	—	—
Radish	0	—	—	—	—

Experiments were carried out in similar cages to discover (1) whether the moth has any preference for one plant over another in selecting foliage on which to lay eggs; and (2) whether it would be possible to attract them from the tomato plants in the glasshouses by planting any particular weed amongst the rows. If such attractive weeds were discovered great benefit might accrue, since they could be sprayed with a poisonous spray throughout the season. Various common garden plants and weeds were planted in pots and boxes, and placed in the cages, where their positions were interchanged every day or two. As far as possible an equal amount of foliage of each variety of plant was included. The moths used were all bred from larvae collected on tomato plants in the nurseries. Five experiments were carried out, in which about a hundred moths were used. The batches of eggs were removed and counted every few days. The results of the experiments are shown in Table II, in which the percentages of the batches of eggs laid on the various plants in each trial are given.

Whenever the common weed "white goosefoot" (*Chenopodium album*) was included, the moths showed a distinct preference for it over the other plants. This preference appears to be about two to one as compared with tomato when equal foliage is exposed. The attraction is insufficiently powerful to give appreciable benefit, since a trap crop could not be a bulky one. Experience subsequently gathered in the nurseries confirms this. *Chenopodium* is a common weed in the houses and, where the infestation is heavy, it is stripped of its foliage by the larvae. Where the infestation is light, it is rarely discovered by the moths. No experiments on a practical scale were therefore carried out on these lines.

(ii) THE EGG.

The egg is flattened and strongly ribbed, without any distinctive markings. Its colour varies at the laying through various shades of green to almost white. During incubation it becomes yellow, and a few hours before hatching, it turns black owing to air entering the shell. The eggs hatched in seven or eight days at mean temperatures varying from 67 to 80° F. All the eggs in a batch hatch within a few hours.

(iii) THE LARVA.

The newly hatched larvae eat part of the egg shells and then commence to feed on the lower surfaces of the leaf on which the eggs were laid. They do not eat completely through the leaf until they are more than a week old. They feed mainly during the night and remain quiescent on the plants in the daytime. At first they drop readily by threads if disturbed, but later this habit is lost. During growth they cast their skins five times, a sixth moult taking place at the pupation.

In its first three skins the larva is always green and may retain this colour throughout its active life. In other cases at the fourth or fifth moult it may take on a lighter or darker shade of brown, and occasionally it becomes somewhat reddish. Yellow larvae and some almost white have also been seen. The skin is closely speckled with white spots, and the hair bases appear as conspicuous black spots on the back and sides. The spiracles are white, with a black spot before and behind, and lie in a bright yellow line which runs the whole length of the body. A line above this, and one along the centre of the back, vary in colour according to the food, as they are merely transparent patches of the skin through which the gut shows: they are usually dark grey. The green and brown forms of the larvae are figured by Buckler, *Noctuae*, Vol. III, Pl. XCIV.

The larvae proved difficult to rear on a diet of tomato foliage alone (Comet variety), though little difficulty was experienced when they were fed on certain other foods. When they hatched on growing tomato plants in large airy cages they scattered from their food in a few days and were unable to find it again. It was necessary to keep them in close contact with the foliage. The most satisfactory method was to place not more than three together on the food plant between plugs of cotton wool in narrow test tubes, and to transfer them to larger tubes as they got older, replacing one of the plugs by a muslin cover. In their last stage they were generally transferred to small plant pots containing earth, and closed by muslin covers. The food was renewed every day or two. In other cases they were sleeved on the growing plant.

Even when these precautions were taken only very small percentages, at most attempts, reached maturity, and in several instances every individual of a batch died. Only once was a large proportion of a batch successfully reared on tomato foliage. Those which succumbed simply ceased to feed and died, unless a change of food was supplied to them. In most cases no recognised disease appeared among them, though the common "flacherie" disease occurred in some. A larva which dies of flacherie has a very characteristic appearance. It becomes an unhealthy white colour, and is soft and readily ruptured if touched. It ceases to feed and remains clinging to the plant by its prolegs. The following day it turns black and falls away in greyish fluid drops. The disease is tolerably common in the houses.

Three of the experiments in rearing will be given in detail.

(*a*) A batch of 135 eggs, laid by a moth reared from a larva collected in a greenhouse, was placed on tomato foliage on beaten earth in a small glass jar covered with muslin. On the fourth day after hatching six of the larvae were isolated in test tubes, and of these, one escaped, three died, and two reached maturity and commenced to spin up on the 35th and 38th days of active life respectively. The pupae were small but healthy, and produced perfect moths. (Of 21 larvae reared on knotgrass under precisely similar conditions, 20 became mature between the 29th and 33rd days of life, and only one died.) The remaining larvae of the batch were kept in the jar and were supplied with fresh tomato foliage every day or two. No disease was apparent, but on the 14th day 25 only remained alive; on the 23rd day 16; on the 38th day, 3, which were all very small. On the 52nd day one was still alive but was very feeble and not one-third grown. It had apparently not fed for some days and appeared to be dying. It was still kept in the same jar and was supplied with knotgrass. The following day it was seen to be feeding on this, and a week later was growing fast. On the 75th day after leaving the egg it became mature and began to spin its cocoon. It was then perfectly healthy and weighed ·96 g., a weight which is above the average of the mature larvae.

(*b*) A small batch of eggs, laid by a moth obtained from the tomato houses, was divided into four equal parts, each part containing about 15 unbroken eggs. When these were about to hatch they were placed on four plants growing in pots, enclosed in muslin sleeves, and kept on the ground in the tomato house. The plants used were knotgrass (*Polygonum aviculare*), white goosefoot (*Chenopodium album*), bittersweet (*Solanum dulcamara*), and tomato. (The bittersweet is the commonest weed in the tomato houses, and one upon which the moth frequently oviposits. The foliage often shows marks where the larvae have fed, but they are very rarely found upon it.) The larvae were transferred to fresh plants during their growth when necessary. After the first week of life they were removed every day or two and weighed, the average weight of those on each plant being plotted in a diagram. The history of these four lots of larvae is as follows:

1. On knotgrass 12 larvae commenced to feed. Their growth was rapid and uninterrupted. One was accidentally crushed and the remainder attained maturity between the 20th and 22nd days of active life. Their growth is represented by the dotted line in Diagram I.

2. On goosefoot nine larvae commenced to feed. Their growth was rapid but rather less so than on knotgrass. Two died without any disease being apparent. The flacherie disease appeared among them and five died of this, two pupating on the 23rd and 27th days of active life.

3. On bittersweet ten larvae commenced to feed and survived the 15th day, growth being very slow but rather more rapid at first than on tomato. They then began to die off though there was no apparent disease. On the 28th day one only survived, and had a weight of ·08 g.; on the 29th day, ·07 g.; on the 30th day, ·055 g. Like the rest of this batch it was apparently starving to death, and though it was transferred

on the 30th day to knotgrass it was too feeble to feed and died the following day.

4. On tomato 12 larvae commenced to feed and growth was very slow. On the 26th day two only remained alive. Of the rest one had died of the flacherie disease and the others of no apparent disease. Of the survivors on this day one weighed ·06 g. and the other ·11 g. The smaller one, which experience showed would have died on a tomato diet, was transferred to knotgrass, and in nine days it outstripped the larger one and then grew rapidly and uninterruptedly, pupating with a weight of ·94 g. on the 50th day of active life. The growth of this larva is represented in Diagram I by the broken line from the point where it was transferred from tomato. The remaining one continued to grow slowly on a diet of tomato foliage till the 46th day, when it ceased to feed for two days and lost weight. A ripe tomato fruit was then supplied to it and it fed readily on this for a few days, subsequently feeding alternately on foliage and fruit. It was not weighed after the 57th day but it was seen to be feeding little and died on the 76th day. The growth of this series fed solely on tomato, is shown in Diagram I by the continuous line, and is in striking contrast to the development on knotgrass.

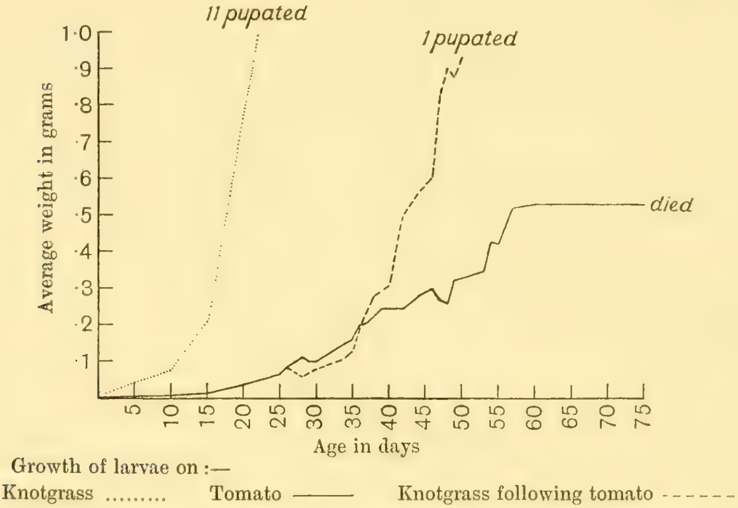

Diagram I. Contrasting the growth of a batch of larvae on *Polygonum* and Tomato.

(*c*) A small batch of eggs, found on *Chenopodium* growing on a rubbish heap in a nursery, was divided into two parts, half being placed on cut *Chenopodium* and half on cut tomato foliage, in glass tubes in a tomato house. Six larvae commenced to feed on the *Chenopodium* and grew rapidly, all maturing between the 24th and 28th days of active life. Their growth is represented by the dotted line in Diagram II. Eight larvae commenced to feed on the tomato foliage, and two of these died without showing signs of disease. The remaining six became mature on the 34th and 35th days. Their growth is represented by the continuous line in Diagram II. Though the development was uninterrupted it occupied on the average nine days longer than on *Chenopodium*.

Larvae were reared from the egg on *Polygonum* and *Chenopodium* and transferred in various stages to tomato foliage and fruit. In ten experiments, 110 larvae, from two to three weeks old, were used in this way. None of these reached maturity, though many of them fed and some made considerable progress. It was not concluded that the larvae in the houses could never pass from these weeds to tomato, but only that such transfer would not be common. On the other hand larvae collected from tomato were very frequently transferred to a diet of *Chenopodium*, *Polygonum*, *Rumex*, cabbage and lettuce, on which foods they invariably matured normally.

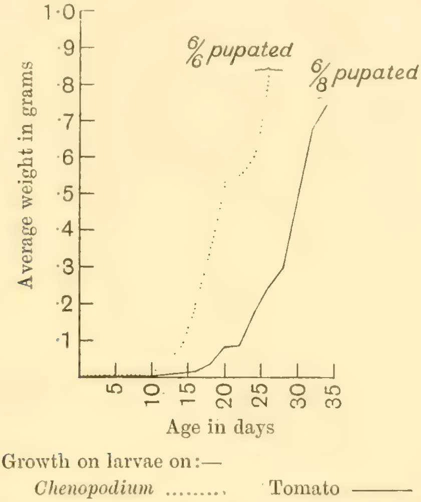

Diagram II. Contrasting the growth of a batch of larvae on *Chenopodium* and tomato.

These experiments are sufficient to show that in some way a diet of tomato foliage alone is not suited to the majority of the larvae, which therefore require a change of food before they can mature. There is also considerable variation in this respect among different batches, and among the individual members of a particular batch. The same phenomenon has been met with rarely in larvae confined to a diet of *Chenopodium*, since occasionally one apparently starved though food was abundant, and conditions healthy. It is of interest that the only other case when an attempt at breeding from the egg failed entirely was on another Solanaceous plant, *S. dulcamara.* This suggests that the heavy death rate on tomato may be due to one or other of the poisons which are characteristic of this group of plants, and to which the majority of the larvae may be not immune. On the other hand the recoveries of the larvae which were transferred from tomato to *Polygonum* recall strongly the recoveries of beri-beri patients when they are supplied with a diet containing the vitamines deficient in their former food. The large death rate may be due to a deficiency in tomato foliage of some substance essential to the maturing of the larvae.

Whatever the cause of this phenomenon it adequately explains why the larvae, though surrounded by abundant tomato foliage in the glass-houses, often leave it and feed on the hard green fruits, and bite into the stems and eat along the pith, in their search for a more suitable diet (see Pl. VIII, figs. 1 and 2). It explains also why the tomato crop in the heavily infested nurseries has not been entirely destroyed. As will be shown presently there are two complete generations and a partial third in the tomato houses in the season, and the offspring of a single pair of moths, emerging in April, might be nearly half-a-million caterpillars in the second generation in August, if all survived; or an average of 30 to each plant over an acre. Such numbers have of course never been attained in any nursery, and as the moths emerge by the hundred to an acre in the heavily infested houses in the Spring, the death rate of the larvae during growth must be enormous. Apparently the young ones scatter in very large numbers from the tomato plants in searching for more suitable food and most of them fail to regain the plants.

The larvae have been successfully reared on *Polygonum* in a cucumber house, but two attempts to rear them from the egg on cucumber foliage failed. In one of these cases 14 larvae from a batch of about 100 eggs passed the first moult and lived eight days, but none survived the second moult and they were all dead on the 11th day. Twenty half-grown larvae which had been collected from tomato plants were fed on cucumber foliage. One of these became a small healthy pupa on the 22nd day after commencing the cucumber diet, two others were then alive but died on the 28th and 29th days respectively, apparently of starvation. The conclusion drawn was that the moth could pass through its life history in a cucumber house if weeds were allowed to grow there, since in all its stages it can survive the high temperature and humidity.

Table III shows the effect of the various food plants employed on the duration of the active life of the larvae, only those which were confined to one diet, and which formed healthy pupae, being included. It shows also that the higher temperatures of the tomato houses increase the rapidity of the development on each food. The average life of the larvae in the houses under natural conditions, estimated by regular counts of them at different stages, appears to be between 35 and 45 days.

Table III. *Showing the effects of various foods and temperatures on the duration of the larval life.*

		Temperatures			Number of	Life in days		
Dates	Place	mean	range	Food	larvae	average	max.	min.
16. v.–15. ix.	Laboratory	66°	50–83°	Tomato	6	39	44	37
				Chenopodium	16	30	34	28
				Polygonum	20	31	33	29
				Rumex	3	32	33	31
12. vi.–8. ix.	Tomato House	72°	52–94°	Tomato	8	35	41	27
				Chenopodium	11	28	35	25
				Polygonum	11	22	23	20
12. viii.–6. ix.	Cucumber House	81°	60–112°	*Polygonum*	9	25	26	24

(iv) THE PUPA.

When full-fed the larvae seek out moderately dry places in which to pupate. Experience in the nurseries shows that they will travel considerable distances in search of suitable sites, and will spin up in crevices in the walls and woodwork, and in sacking, or sometimes among the leaves of the plants. On a heavy wet clay soil most of them pupate in the structure of the glasshouse, but where the soil is light and friable the majority pupate there, especially under the pipes or round the concrete piers. The pupae are frequently found in the mulch, or just below it, and very rarely indeed at a greater depth in the ground than one inch. They are often seen in the unfaced joints of the pipes, and in the tops of the canes used for plant staking. In such places the larvae spin light silken cocoons and remain quiescent for two or three days before pupating. The pupa is smooth, shining, and normally almost black, though occasionally lighter specimens are seen.

The period during which the insect remains in the pupal stage varies very considerably. It is known that in nature there is often a partial second flight of this moth in the autumn. This is derived from the larvae which become full-fed in July and August, some of which produce moths in three or four weeks in warm years, while others do not respond to the favourable temperatures but remain as pupae till the following summer. If the autumn proves unfavourable to the second flight and none of their offspring survive to maturity, those which have not emerged carry on the species the following year. Although the temperatures in the tomato houses are fairly equable from the beginning of spring to the end of autumn the same phenomenon is seen and the response of the pupae to the favourable temperatures varies.

The history of the pupae which were observed in the tomato house and the laboratory is given in Table IV. Those which were kept in the greenhouse were in the shade under the staging and were, for the most part, on moist soil in glass jars. A thermometer was kept among them and the temperatures were recorded daily. Those in the laboratory were in similar jars out of the sun. The table shows the mean, absolute maximum and absolute minimum temperatures for each month. It also shows the number of pupae which pupated in each month; the numbers of these from which moths emerged after shorter or longer periods, with the possible limits of these periods in brackets; and a note on the pupae not accounted for in the previous columns. It will be seen that the pupae in the laboratory behaved similarly to those in the greenhouse, in spite of the fact that they were exposed to somewhat lower temperatures. On the average the pupation period in the laboratory was slightly prolonged, and it was evident that there is some factor in addition to temperature which partially influences the period. An account of those kept continuously in the tomato house follows.

None of those which pupated at the end of April produced moths in the shorter period, but most of them emerged in a period varying from 100 to 200 days. All but one of those which pupated in May emerged in a short period (17–31 days). The one which delayed its emergence in this month became a moth about the 122nd day. All those which pupated in June became moths after a short time (20–50 days), but took on the average rather longer than the May pupae. This was probably due to a spell of cold weather at the end of the month when the temperature in the greenhouse fell to 54° F. on several occasions. Prolonged pupation was again in evidence among the July pupae, as three-quarters of them emerged in less than 35 days, and the remainder have not produced moths up to the end of November, 120–150 days after their pupation. In August only 17 per cent. emerged in the short period (17–32 days), and 83 per cent. are still pupae after 90–120 days. These were exposed throughout the first 60 days after their pupation to a higher temperature than those which pupated in the laboratory in June, though the latter all emerged in the short period. None of those which pupated in September have yet produced moths.

Table IV. *Showing the behaviour of the pupae from April to November, and the partial influence of temperature on the pupation period.*

		Temperatures			No. of moths which emerged after		
	Month	Mean	Range	No. of pupae	Short period	Long period	Nos. which remain pupae, or died
Tomato House	April	—	—	11	0	10 (102–200 days)	1 after 200 days
	May	73·2°	58–89°	85	82 (17–31 days)	1 (122 days)	2 died
	June	70·9°	54–90°	65	63 (20–50 „)	0	2 died
	July	70·8°	54–90°	30	23 (16–35 „)	—	7 after 120–150 days
	August	71·3°	52–94°	110	37 (17–32 „)	—	73 „ 90–120 „
	September	70·7°	52–90°	15	0	—	15 „ 60–90 „
	October	63·3°	48–79°				
Laboratory	May	65·0°	56–76°	20	20 (24–35 „)	0	
	June	64·2°	50–82°	23	23 (28–43 „)	0	
	July	64·7°	52–77°	2	2 (20–22 „)	0	
	August	68·2°	53–83°	39	6 (23–35 „)	—	33 after 90–120 days
	September	64·5°	44–82°				

The influence of the temperature on the pupation period was investigated in the following experiments. Mr Bacot exposed pupae and mature larvae to low temperatures in the cool and cold rooms at the Lister Institute at Chelsea during August. The pupae were chilled by exposure for one week to a temperature of 54° F. (50–59°), followed by a week at 31·5° (28–35°); they were then kept in the laboratory for three weeks, and finally returned to the greenhouse. The mature larvae were exposed for a fortnight at 54° F., but not to a freezing temperature, and they pupated during this time. They were then returned to the laboratory and greenhouse with the other chilled pupae. Control pupae and larvae had been kept continuously in the tomato house.

One of those chilled had pupated the last week in April, and the moth emerged five days after its return to the greenhouse. The pupation period was 141 days, midway between the limits of the emergences of the controls (102–200 days), so no effect from the chilling is apparent in this case.

Twelve pupae which had pupated at the end of July and the beginning of August were chilled, and three moths emerged from these after their return to the tomato house, with pupation periods of 38–40 days. Six out of the 12 control pupae produced moths with pupation periods of 20–32 days. In this case the chilling prolonged by about a week the short pupation period of those which have emerged, and apparently increased the tendency of the others to delay their emergence, nine of those chilled, as against six of those unchilled, being still pupae after 100 days.

The three mature larvae which pupated in the cool room have not emerged after 110 days, while in the control series of eight pupae obtained from the same batch of larvae, three emerged after 17–23 days, and five remain in the pupal stage. The chilling in this case seems to have prevented the early emergence of any of the moths.

In another experiment 30 pupae which had pupated August 1–5 were divided into three lots of ten each and placed on moist earth in the usual jars. One of these was put into a cucumber house, one into a tomato house, and the third out of doors under a wooden box covered by a folded heavy sack. The temperatures are given for the first month following the pupation. That in the cucumber house was 70·4° (Range 59–104°), and of the ten pupae eight emerged after periods of 18–22 days, one died, and one is still a pupa, after 120 days. In the tomato house the temperature was 71·3° (Range 52–94°), and four pupae emerged after 20–25 days, six still remaining in the pupal state. The temperature to which those outside were exposed was 66·9° (Range 42–97°), and one only emerged after a period of about 24 days, and the rest are still pupae. The influence of the temperature was thus very marked, but the tendency to prolong pupation was not abolished even by the relatively hot conditions of the cucumber house.

Some moths thus emerged in less than 50 days, and some after more than 100 days, but there were no emergences between these limits. At the end of April the glasshouses in this district were covered by snow for two days, and the consequent chill probably accounts for the long pupation periods of those insects which were nearly mature larvae at that time. The tendency to prolong pupation reappeared in the middle of a warm summer and became more intensified as the year went on. Those responding to it correspond to those individuals of the first brood in nature which do not emerge to form part of the autumn flight of moths, but remain as pupae from the end of one summer to the beginning of the next. Each pupa has thus an inherent tendency either to emerge quickly or to hibernate. The experiments show that an artificial raising of the temperature may reduce the tendency to hibernation, but fails to abolish it in all within the limits tested. An artificial cooling may intensify it, or even make it total. The susceptible period in the insect's life is in the late larval and early pupal condition.

At the commencement of this work, judging by what was known at that time, it appeared that it might be possible to force all to emerge from the pupae by keeping up the temperatures of the greenhouses at the end of the growing season when there is no food for the larvae in the houses, and that the moths could then be destroyed by fumigating. The foregoing facts show that this is impracticable as the pupae would resist forcing at any temperatures to which the tomato houses could be raised.

[The following note completes the history of the pupae kept under observation through the winter in a greenhouse continuously heated. No moths emerged from September 5 to December 10, and very few in the latter month and in January. There was little relation between the dates of pupation and the dates of emergence of the moths. The longest pupation period was about 300 days (August to May). Those which had not emerged by the end of May were found to be dead.

No. of moths which emerged in	Mean Temp.	Pupated in July	August	September
December	60·6°	1	1	0
January	62·9°	1	3	4
February	63·2°	0	34	49
March	66·3°	3	34	74
April	66·8°	0	6	50
May	74·7°	0	2	15]

3. THE INFESTATION.

In captivity the shortest entire life cycle from moth to moth, when the larva was fed on tomato foliage, was 55 days. The eggs were laid on July 4; hatched on July 11 (7 days); larva matured and burrowed on August 6 (27 days); pupated August 8 (2 days); moth emerged August 27 (19 days). The mean temperature during this time was 72° F. (Range 52–94°). The life cycle under natural conditions in the tomato houses occupied rather longer on the average.

The life history of the insect was studied by the systematic examination of the 1600 plants in a 200-foot house from the end of April to the middle of September. This house was heated up in January and used for propagating one lot of plants in the early part of the year. It was planted out the second week in April. For the purposes of this experiment it was isolated from the rest of the block by a stretch of hessian dropped from the gutter and fastened to a board running along the ground, the flight of moths to the rest of the block being thus prevented. The plants were not sprayed.

The plants were examined at intervals of three or four days. When they were small the examinations were made leaf by leaf, but when this became impracticable it was made plant by plant, attention being drawn to the presence of larvae by marks of recent feeding or by fresh droppings. All found were removed. Eggs, and larvae up to a week old, were counted as batches, and scattered larvae were counted individually and classified into two groups: (1) as "young" larvae, up to an age of about three weeks, and (2) as "old" larvae, which had passed the fourth moult. The numbers collected weekly in the two collections were plotted in a diagrammatic manner, the eggs being included with the newly emerged larvae in the week following their collection.

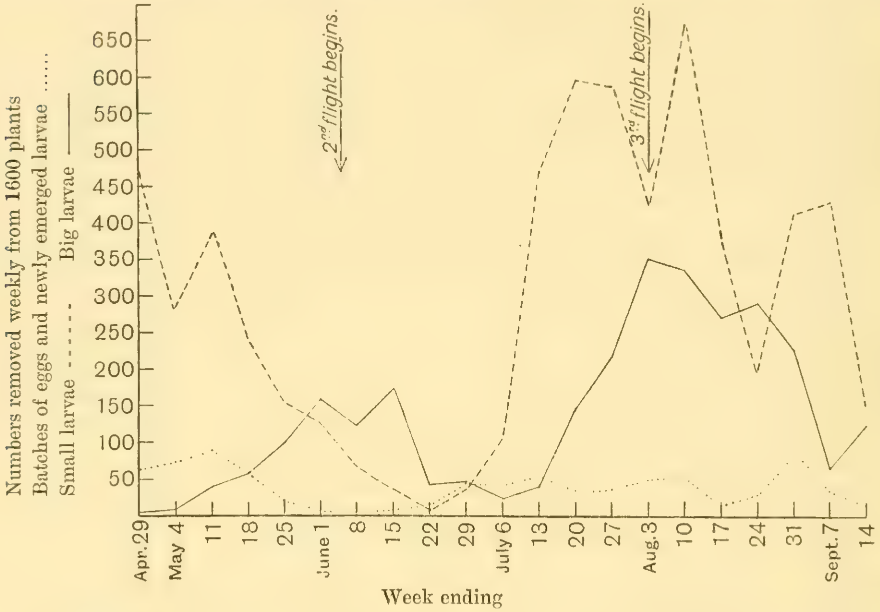

Diagram III. Showing the rise and fall in the numbers of larvae in the successive generations.

Diagram III thus shows the history of the pest over a period of four months, the numbers of larvae being of course much reduced by hand-picking. The dotted line represents the newly emerged larvae, the broken line the young larvae, and the continuous line the ones which were nearly mature. The numbers of the newly-emerged fell to a minimum about June 8, and then again increased, and a similar fall and rise occurred about August 17. These dates represent approximately the beginning of the second and third broods of larvae of the year respectively. The numbers of old larvae fell to minima about July 6 and September 7, and this indicates that the first and second broods ended about these dates. As the infestation was getting out of hand in August moth trapping was resorted to in the house, and 174 moths were caught in this month, the numbers of larvae being much reduced at the end of the month in consequence. It has been known that there are two broods of larvae annually in the houses, since the reduction in numbers between these, as represented in the diagram at the end of June, is very noticeable to the observant grower. It has been a disputed point whether there is a third brood, but a study of the diagram shows that there is no doubt about this, at any rate in a favourable year. When the mature larvae fall to a minimum at the beginning of September the growing larvae of the third brood are very numerous and the demarcation between the broods is thus obscured.

The moths commence to emerge during February in houses heated up in January, as in the house under consideration. The emergence of the first flight continues to the end of May, and possibly later, being at a maximum about the beginning of this month. The reasons why this flight is so prolonged are: (1) the pupae do not respond equally to favourable temperatures; (2) they are in very different situations in the houses, some being close to the pipes, and some almost at the temperature of the outside air.

The moths of the second flight began to emerge from pupae bred from the first brood of larvae on June 4, while moths which were the offspring of these commenced to emerge the first week in August, the exact date being obscured by the slight overlapping of the second flight. Probably all the pupae which survive the winter produce moths which take part in the first flight. The very large majority of the offspring of these form the second flight, only a few delaying emergence, and probably none in a uniformly warm spring. About a quarter of the offspring of the second flight took part in the third flight in the present year, while the remaining three-quarters delayed emergence. In a cold year the second flight of moths might be so late that none of their offspring would emerge to form a third generation.

4. ORIGIN AND METHOD OF DISPERSAL.

There are three ways in which the pest may be introduced. Firstly, seedlings carrying the eggs or young larvae may be purchased from an infested nursery. Secondly, market baskets may bring in the pupae. Cases of both these are known, and they are sufficient to account for its appearance in new localities, supposing that it originated in only one place. Thirdly, the moth itself may enter through broken panes or open ventilators.

An experiment was carried out to discover to what extent this moth does enter the greenhouses. A block of seven 200-foot houses which had been used for propagating two lots of seedlings, was finally planted out the first week in May. The two houses at the east end of the block were isolated from the others by means of a sheet of hessian, and were made moth proof. Porches of hessian, with tightly fitting second doors, were built over the entrances at one end, while the doors at the other end were nailed up and caulked. The building was overhauled and put in perfect repair. The roof ventilators were screened with tinned steel woven wire, the mesh of which was one-sixth of an inch square. The large ventilators over the doors were replaced by cones of the wire mesh, which were directed downwards into the houses, and ended in sleeves of calico to which were attached glass jars half filled with water. In screening the roof ventilators it was necessary to arrange the wire in the form of bags in which the gear could work freely. In one of the houses these bags were completely closed, and in the other, one end of each opened into a calico sleeve which dropped into the interior of the house and opened into a glass jar of water. The sleeves were 18 ins. long, 6 ins. in diameter at the top, and 3 ins. at the bottom. This arrangement was devised under the impression, then generally held, that the moths invaded the houses in large numbers. The writer was informed that sometimes four or five were found jammed in the cracks around a door and agreed with the natural conclusion that they were trying to force their way in. The jars were arranged to trap moths deliberately trying to enter the houses, as it was thought that in trying to reach the plants below they would pass down the sleeves and be caught in the water. It is now known that the moths caught in the cracks were endeavouring to force their way out, and the experiment from this point of view was badly devised. The screening was not completed till June 14 owing to the difficulty of obtaining material (see Pl. IX, fig. 3).

A female *H. oleracea* was found in one of the jar traps on July 30, and a dead male inside one of the screens on August 20. On the latter date 16 of the jars were replaced by shallow dishes, 4 ins. in diameter, filled with tanglefoot. These were placed at the tops of the calico sleeves which were tied below to keep them in position. At the end of September these traps were examined and four moths were found in them, three being *H. oleracea*, two females and one male, and the other a common Noctuid, *Mamestra brassicae*. It was thus proved that moths do pass into the houses in infested nurseries, though the method failed to give any estimate of the numbers of the invaders. The comparison of the infestations of the screened and the unscreened parts of the block confirmed this. It was not possible to destroy entirely the first brood of larvae, and some infestation was expected in all the houses from the offspring of these. Very few larvae were found until July 25, when in the two screened houses four mature ones were seen, and in two houses in the unscreened part, four batches of newly-emerged and seven older ones were found. On August 26 and September 10 an examination of the two screened houses gave 12 batches of newly emerged larvae and 164 older ones, and at about the same time on an equal number of plants in the unscreened part there were found 22 batches of newly-emerged and 689 older ones. Judging by these figures there were in August more moths to the house in the unscreened than in the screened part.

Table V. *Showing that the pest is a spreading one in the Lea Valley.*

Area	No. of Reports received	Average No. of years since tomatoes were first grown under glass	Average No. of years since the pest was first seen	Average No. of years since it became serious
Enfield Highway	7	19	14	12
Freezywater	3	16	11	10
Waltham Cross	6	17	11	7
Cheshunt	8	11	7	4
Flamstead End	6	17	4	2
Broxbourne	2	21	8	5
Hoddesdon	4	14	7	2
Ware	2	16	6	1
Waltham Abbey	5	12	9	5
Sewardstone	5	11	6	3

If it were a normal habit of this common moth deliberately to enter glasshouses and to breed upon tomatoes all the nurseries should have become infested soon after their institution, since it is very generally distributed. The history of the pest in the Lea Valley shows that this has not been the case. The growers have been questioned on the origin of the pest in their particular nurseries and the answers received are summarised in Table V. In the first column the Lea Valley is divided up into areas, and the second gives the number of definite replies received from these. The remaining columns show the average number of years since: (1) tomatoes were first grown under glass; (2) the caterpillar was first seen in the houses; (3) it became a serious pest.

There is no gradation in the numbers in the third column, the industry having been established a considerable number of years throughout the district. The numbers in the last two columns show a distinct gradation, which bears a close relation to the relative positions of the areas. The earliest records are at Enfield Highway. From here it seems to have spread rapidly through the congested area of nurseries which follows the main road through Freezywater to Waltham Cross. The first records from the other localities are: Cheshunt 1908, Broxbourne before 1911 (indefinite), Hoddesdon 1909, Ware 1914. In the more outlying districts the earliest records are: Waltham Abbey 1906, Sewardstone 1911, Chingford 1913: and to the west of Cheshunt, in the Hammond Street and Flamstead End district, 1914.

It has therefore spread like an epidemic disease. Where the nurseries are congested it has moved rapidly, and where there is a gap it has lingered. In places it has made sudden jumps, for which the basket method of spread would account.

The moths which commence the infestation in each nursery are thus derived in some way from another nursery in which the pest is already established. In congested areas it may be that they are the actual moths which have escaped from infested houses, or they may be the offspring of such. The efforts of the insects to escape are so persistent that it is certain that a large proportion of those that emerge in the houses must succeed in doing so. These will naturally breed on suitable vegetation around the nursery, and as they are passing out in April and May, before the moth normally flies in nature, there is ample time for them to have a large or total second generation in the late summer of a favourable year. In the immediate neighbourhood an increase of the species will result from this which will readily encroach on adjoining nurseries. Several species of common butterflies and moths frequently blunder into the greenhouses and may be seen beating against the panes in their efforts to escape again. The more plentiful the species becomes the more likely are individuals to blunder in, and if it becomes excessively common the entry of a few each year becomes a certainty, since the total area of the ventilator openings is large. The escaping moths would thus account for the increase and the consequent spread.

This explanation of the spread of the pest, though difficult to prove conclusively, seems to be the most reasonable one, since it presupposes no modification of the instincts of the moth which cause it deliberately to invade places which it apparently dislikes, and to lay its eggs on foliage to which many of its larvae are unsuited.

The species outside is checked normally by a variety of factors: unfavourable weather; severe winters; the ravages of bats, birds, shrews, moles, toads and other animals; the attacks of hymenopterous and dipterous parasites. In the houses the climatic conditions are equable from early spring to late autumn, and the pupae are protected from the severity of the winter. Enemies are relatively few, the only important ones being spiders, the carnivorous beetle, *Carabus granulatus* L. and the ichneumon parasite, *Pimpla instigator* Fabr. The last of these, though of great benefit, loses much of its importance since it fails to keep pace with the rapid generations of the moth. These unnatural conditions foster those larvae which find tomato foliage a suitable diet, and this, together with the fact that the moth is a very prolific one, has enabled it to become a very serious pest in circumstances which are otherwise against it.

The moth is therefore not a normal pest of tomatoes and is much less firmly established in the houses than it at first sight appears to be. There is a danger that it will become a normal pest unless it is stamped out while it is still in some respects weak. If the methods adopted to control it are merely sufficient to bring its ravages within small dimensions its disappearance is not to be expected, and the cost of this partial checking must be regarded as a perpetual annual tax on the tomato industry.

5. CONTROL.

The instructions which follow have been framed with a view to the complete abolition of the pest, by attacking it in all its stages in the houses, and by preventing the escape of the moths to the outside, as far as this is reasonably possible, so that conditions around the nurseries may again become normal. If all the growers will carry out these instructions for a few years it is believed that the pest will cease to exist among them, but since the infection spreads in congested areas, the neglect of one will neutralise the efforts of the others from this point of view.

In order to effect this it is necessary that: (i) the larvae should be destroyed by spraying; (ii) larvae which appear when spraying is not practicable should be trapped; (iii) the moths should be trapped throughout the season; (iv) pupae should be destroyed; (v) certain unnecessary conditions favourable to the insect should be avoided. These will be discussed in turn.

(i) SPRAYING.

Substances which are stomach poisons to the larvae should be used for this. They remain effective for a long time on plants protected from the rain, and are more certain than contact poisons. Suspensions of arsenate of lead paste, with a composition covered by a guarantee from the makers, should be used on young plants. It does not harm the foliage or prevent the setting of the fruit, and is a very stable substance. Paris green, though an effective poison for the larvae, is liable to damage the plants. Vegetable poisons, such as hellebore and nicotine, are costly for wholesale spraying. The sample of lead arsenate paste used in these experiments was guaranteed by the makers to contain 20 per cent. of arsenic pentoxide (As_2O_5).

As the arsenate is very heavy it sinks rapidly out of suspension unless very thoroughly agitated. It is liable to leave the machine at the correct strength at first. After a few rows have been sprayed it becomes too weak to be effective. Finally when the machine is nearly empty it becomes wastefully strong. The only kind of agitation that is quite efficient is constant shaking, and as this is difficult when the spray is being applied, some substance should be added to the water which will hold the substance up throughout the operation. A convenient and effective material to use is saponin, and it is economical as very little is necessary. It should be added to the water at the rate of 2 ounces in 100 gallons, or a small half-teaspoonful in 2 gallons. The paste should be mixed with a little of this solution and the thin cream obtained should be added to the bulk. Little agitation is then necessary to keep the suspension even until the machine is empty, and the spray will run in an even film which completely covers the foliage.

As an alternative to saponin the following spreader could be used. Slake 2 ounces of calcium oxide and suspend it in half-a-pint of water: work one ounce of casein into a cream and suspend it in a second half-a-pint of water: add one-third of this mixture to each 2 gallons of spray. This is approximately one pound of casein to 100 gallons of water. The spreader has been tested on a large scale at the rate of $\frac{1}{2}$, 1 and 2 lbs. of casein respectively to 100 gallons. The second concentration is an effective spreader but it is more costly in use than saponin at present prices and is more trouble to mix. It should therefore not be used when saponin can be obtained.

Table VI. *Comparing the death date of the larvae on tomato plants sprayed with suspensions of lead arsenate paste* (20 *per cent.* As_2O_5) *of various strengths.*

Lbs. per 100 gals.		2	3	4	5	6	10
No. of larvae used		52	115	156	165	176	77
No. of larvae which pupated ...		18	2	7	4	4	2
Percentages surviving on succeeding days	1	97·1	94·6	90·2	82·9	84·7	85·3
	2	82·4	67·2	71·5	47·2	49·3	54·6
	3	61·8	46·0	37·3	19·3	28·4	22·6
	4	47·1	19·5	20·6	8·4	12·1	11·9
	5	35·4	13·3	8·5	6·6	5·8	3·9
	6	29·5	9·8	5·2	4·8	2·3	2·6
	7	26·6	7·1	3·9	3·6	1·7	0
	8	17·7	3·6	1·9	3·0	·6	—
	9	14·8	3·6	·6	2·4	0	—
	10	11·9	1·8	0	1·2	—	—
	11	6·0	·9	—	0	—	—
	12	6·0	·9	—	—	—	—
	13	3·1	0	—	—	—	—
	14	0	—	—	—	—	—

The larvae die off gradually when the lead arsenate is used at a strength of 2 lbs. to 100 gallons, or stronger. Some are found dead the day after the spraying but others survive a week or more. This is probably because they find the poison distasteful and the majority cease feeding before they have taken a fatal dose. After a time hunger forces them to recommence feeding, until finally a fatal dose is taken. In order to discover what concentration should be employed, small bushy plants in pots were sprayed with various strengths, from 2 to 10 lbs. of the paste to 100 gallons. When the spray was dry the plants were infested with a large number of larvae collected in the tomato houses. Half grown to mature ones were employed and they were kept from wandering either by enclosing the plants in muslin sleeves, or by placing them in large vessels covered with cloth. They were examined daily and the dead larvae were counted and removed. In each case a few of the larvae pupated but the varying numbers of these have little significance, as they were probably fully fed when placed on the sprayed plants. Two tests were made for each strength from 3 to 6 lbs. to 100 gallons and one test at strengths of 2 and 10 lbs. respectively. The results are given in Table VI, which shows under each strength the number of larvae employed and the percentages of these which survived the succeeding days. If these numbers are traced down the columns and compared day by day it will be seen that there is a considerable advantage in using the substance at a greater strength than 3 lbs. to 100 gallons, while between 5 and 10 lbs. there is probably no more variation than could be accounted for by experimental error. However as the plants were considerably damaged by the feeding when the weaker concentrations were used, and at strengths of 6 and 10 lbs. only traces of feeding were seen, it is recommended that a concentration of 6 lbs. of the paste in 100 gallons should be employed. There is no advantage in using it at a greater strength.

A knapsack sprayer is quite efficient if saponin is used, and it was found that a man using one of these machines could easily keep pace with the planting over 25 acres of plants. The spray should fall downwards onto the foliage, and the operator should wear a piece of muslin over the face to prevent the poison getting into the eyes and nose. The plants should not be watered until the following day when the spray is thoroughly dry.

If larvae are seen feeding in the propagating houses the plants should be sprayed at once. In the houses known to be infested they should always be sprayed shortly after planting out. Another spraying should be carried out about a month before fruit picking will commence. This is the most important application and should be done in every block in the nursery where there has been any caterpillar in the previous year. It is a mistake to delay this final spraying because no larvae are seen feeding, as the arsenate cannot be employed on older plants without prejudice to the industry, and they may appear for the first time after it is too late. The grower will then be left with no remedy except picking off the insects by hand. This spray not only kills the larvae present when it is applied, but also all that subsequently feed on foliage that has been efficiently treated.

As some of the growers have been reluctant to adopt spraying, it seemed desirable to obtain practical proofs of this method of control over hand-picking. Reference was made above to a 200-foot house (one-tenth of an acre) which was isolated from the rest of the block by a stretch of hessian dropped from the gutter to prevent the passage of moths. The 1600 plants were untreated while those in the remainder of the block were sprayed twice with arsenate of lead. Each of the unsprayed plants was examined twice weekly and all larvae found were counted and destroyed. From four to six hours a week were devoted to this work—almost the equivalent of the entire time of one man over an acre of plants. The work was therefore more thoroughly done than would be possible in a trade nursery. In spite of this, very poor control was kept, as only a small proportion of the larvae present were discovered at any one examination. Many matured and pupated, so that the summer brood was as large as the spring one. Much fruit was bitten and many stems were eaten through. The adjoining house was first examined on May 1, a fortnight after the plants were put out, and 79 larvae were counted to each hundred plants. These were not removed and a few days later the house was sprayed with arsenate of lead, the operation occupying one hour, and 10 gallons of diluted spray being used. Two days later it was again examined and 26 larvae were counted to each hundred plants. Ten days after this another count gave four larvae to the hundred plants. It then received its second spraying as before and no more larvae were seen until June 21, and from that time on, till the comparison was stopped at the end of July, very few were seen, though later in the season they became more numerous.

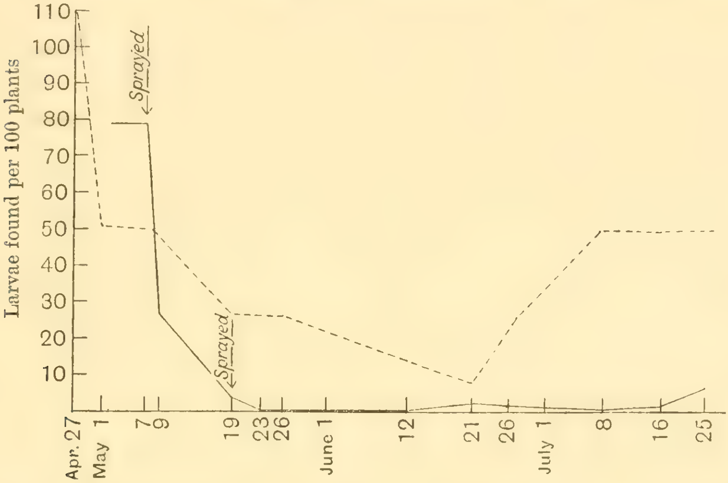

Diagram IV. Contrasting the control effected by hand-picking -------- and spraying with arsenate of lead ———.

Diagram IV shows the results of this experiment in a graphical manner. The continuous line represents the number of larvae found to the 100 sprayed plants in each of the 10 examinations made. The dotted line shows the number removed from each 100 plants in the unsprayed house on approximately the same dates. The hand-picking during these three months occupied over 70 hours and was inefficient. The spraying cost an insignificant sum, occupied two hours to each house, and secured effective control for half the growing season.

This block was heated up in January and used for propagating. Consequently it was planted late and it was possible to give it the second spraying well on in May. When plants are put out in March to give early fruit at the beginning of June the second spraying could not be done after the end of April. As the blocks which receive these plants are usually unheated till the beginning of March, the first moths are later than in the case just considered. They will therefore be still emerging in numbers when there is much new unprotected growth on the plants, and the control will be less thorough than that described. This explains why those growers who have used the arsenate have found that, in spite of it, a few larvae are seen fully fed at the end of June. The offspring of these, and possibly of a few moths that have entered from outside, cause a heavy infestation in August and September, though less heavy than where spraying is not practised. It is therefore necessary to employ additional means of control.

Experiments were made with tuba root (*Derris*), a quantity of which was obtained by Mr Fryer, Entomologist to the Board of Agriculture. The specimens tested were prepared by Mr Tattersfield of the Rothamsted Experimental Station. In ordinary use this substance is said to be not poisonous to man and it could be used on plants in any stage. It was tested in several ways: (1) as a dry dust, alone and in dilution with powdered earth; (2) with saponin in watery suspensions, at various strengths from ·25 per cent. to 10 per cent. by weight of the powdered root, mixed and strained through muslin; (3) with saponin in watery suspensions of an alcoholic extract (six times the strength of the powdered root) at various strengths from ·08 per cent. to 2 per cent. by weight.

Tomato plants in pots were dusted or sprayed with these and infested with larvae collected in the nurseries. The dusting was unsatisfactory as it made the plants dirty and encouraged the growth of moulds. It need not be discussed further. The watery suspensions of the powdered root killed the larvae at a 10 per cent. strength, but a 5 per cent. strength failed to do so within a reasonable time. These strong mixtures also dirtied the foliage. Suspensions of the alcoholic extract proved very satisfactory sprays on an experimental scale. A series of 18 experiments showed that one part of this substance by weight in a thousand parts of water is a sufficiently potent spray. A plant sprayed with this was infested with 12 half-grown larvae which were confined to one leaf by means of a sleeve. Two days later seven of these were dead, and eight days after they were put on they were all dead. Ten more half-grown larvae were then placed on another leaf, and ten days later these were all dead. The spray therefore remained potent for 20 days. The foliage of the plant was not damaged and the fruit set normally. This plant at the end of the experiment was photographed with a control plant of the same age which, without spraying, was infested with 10 half-grown larvae at the time the second lot were released on the sprayed plant. They completely ate a leaf each day and had destroyed the plant by the time those on the protected one were all dead (see Pl. IX, fig. 4). Similar experiments were carried out with strengths of 5, $2\frac{1}{2}$, $1\frac{2}{3}$, $1\frac{1}{4}$ and $\frac{5}{8}$ lbs. of the alcoholic extract in 100 gallons of water respectively, and each plant was infested with 22 larvae as described above. The results varied little from those detailed, except that with the weakest strength the death-rate was somewhat slower. None of the plants were damaged and the substance therefore appears to be safe to use, but no large scale experiments were carried out. At present there are no supplies of this substance available in England. Should it become available in large quantities it will prove a very useful adjunct to the arsenate of lead for later spraying. When the foliage of the plants becomes dense however treatment becomes more difficult, and will prove less effective in consequence.

(ii) LARVA TRAPPING.

When spraying is not practicable the infestation may be reduced by trapping the mature larvae by means of sacks. They travel considerable distances in seeking suitable places in which to pupate, and sacking proves very attractive to them. Sacks placed about the houses will therefore catch a surprising number. They should be loosely folded and placed on the pipes under the gutters, or on the lower wires and touching the woodwork. Naturally the more used the better, but four or five to a house will collect hundreds of pupae in a moderately infested block. A count of them in 11 sacks, distributed in three houses and left for three weeks in September, gave a total of 729, or 66 to a sack (see Pl. X, fig. 5).

It is a long and tedious business to remove the larvae and pupae from them by hand, and it will be found more economical and thorough to collect them in a barrow and to dip them for half-a-minute into a cauldron of boiling water, and then to shake them. This will kill all the pupae, and also the wireworm beetles and the vast swarms of wood-lice which also find sacking attractive. They should be collected and dipped every 21st day. If they are left longer moths may begin to emerge.

(iii) MOTH TRAPPING.

The trapping of the moths is as essential as the spraying. It is important that the escape of the moths to the outside should be prevented as far as possible, as they are responsible for the spread of the pest to neighbouring nurseries, and their offspring may re-enter the houses when the plants are not protected by the spraying. Trapping will not entirely prevent this escape but it must reduce it greatly. Apart from this, immediate advantage follows. The moth is long lived and can lay ten batches of eggs. As many of them may be caught soon after they leave the pupae the laying of most, or in some cases all, of these can be prevented.

The moths show no reaction to any lights which have been tested (candle flames, oil and acetylene lamps) and it is therefore necessary to attract them by baits. These are best exposed in jars which are tolerably deep in proportion to the width, have a pronounced shoulder, and a mouth opening about 2 inches across. Glass fruit preserving jars were found to answer well, the dimensions being, depth 8 ins., diameter 3 ins., width of neck 2 ins.

A fermenting mixture of crushed ripe tomato, water and yeast, was first tested as a bait in the houses, and a few moths were caught by this means. Five jars containing this mixture were hung on the wires near the gutters, and five others, each containing about three ounces of a mixture of ale and treacle, were placed in contrasting positions on the other sides of the gutters. In two nights the latter caught 52 moths, while the tomato traps caught only seven. Three jars of the following baits were then prepared: (1) ale alone; (2) treacle, one part; water, two parts; (3) treacle, one part; ale, two parts. One jar of each of these was placed in each of three houses and exposed for a fortnight. The distance between the traps was 100 feet, and their positions were interchanged twice during the exposure to equalise the chance of each bait. The numbers of moths caught were as follows: ale alone, 14; treacle and water, 12; treacle and ale, 109. The last of these was thus proved to be a very effective bait and was used in all subsequent trappings, a good quality dark treacle (present retail price, 9*d.* a pound) and ordinary cheap ale being employed. Waste beer was used in one set of traps but was found to be less effective, as the débris floated and formed a platform on which the moths could rest to feed, and escape. Even with the mixture usually employed it was found that some of the moths escaped after feeding, as a few were caught by hand in the houses and were found to be distended with the bait. As it is necessary to have a moth trap widely open to allow the insects to flutter in it is difficult to prevent their escape by mechanical means, and it was therefore decided to poison the mixture.

Laboratory tests were made with sodium fluoride, $\frac{1}{4}$–1 per cent.; sodium arsenite, 2 per cent.; and lead arsenate paste, 2 per cent.; each mixed with ale and treacle and soaked up in muslin. These were placed in moth cages which included growing tomato plants and newly emerged moths. In the laboratory (T. 64° F.) the moths died off slowly. For example in the case of 1 per cent. sodium fluoride the average life of 20 moths was 7·5 days (4–10 days). In the tomato house (T. 70° F.) with the same poison the average life was 2·5 days (1–5 days). The probable explanation of this difference is that at the higher temperature the moths drink more freely. Exposed to 2 per cent. sodium arsenite in the tomato house, five moths had an average life of 3·6 days (1–5 days). 2 per cent. lead arsenate paste was found to be ineffective in the laboratory, eight moths all surviving six days, when the experiment was stopped. This study of moth poisoning was not completed when the number of available moths became too small for its continuance. When sodium fluoride was tested in the laboratory very considerable numbers of eggs were laid by the moths after they had taken the poison, but these were scattered all over the foliage and cage in ones and twos, and not in the normal large batches. One of the jars containing the ale, treacle and sodium fluoride was placed in a moth cage in a tomato house, and 11 newly emerged moths were released in it. All were caught the first night and no eggs were laid. The experiment was repeated with five moths, and four were caught the first night, while the remaining one, a male, was found in the trap on the third day. The moths are thus caught before they have laid any eggs in many cases, and the majority trapped in the houses were fresh specimens which had obviously flown little. However as a few eggs might be laid in the intervals between escape and death, the escape should be prevented as far as possible. The poison prevents fermentation and retards the formation of a scum on the fluid, and the dead bodies should be removed occasionally so that they do not form a platform.

Sodium fluoride is not a perfect poison and further search for a more effective one will be made. It has the advantage that it is not at all dangerous in use, and its employment in the greenhouses will ensure the early death of any moths which feed and escape from the jars.

Wholesale moth trapping was carried out in a block of 12 200-foot houses. The plants had not been sprayed and no organised hand-picking had been practised. The first brood of larvae was at its maximum about the last week in May, and the second about the third week in July. It was then the most heavily infested of the 12 blocks in the nursery. The foreman in charge thought that it would be necessary to put all the hands available at the work of hand picking the larvae in order to save the crop. Experimental trapping with various baits had been commenced in June on a small scale, and at the beginning of July three traps baited with ale and treacle were placed in each house, one at each end and one in the middle, suspended from the wires near the gutters. This system of trapping was continued to the end of the season, with the exception of a fortnight at the beginning of August when all but four of the jars were removed and replaced by 72 pieces of muslin soaked in the bait to which 1 per cent. sodium fluoride was added. This method was considered unsatisfactory as, though the initial outlay is less, the attention required by them is greater than in the case of the jars, and as shown above a poisoned moth may lay a few eggs. Also no dead moths could be found, and it was thought that the growers would have more confidence in a method, the results of which were evident. When the full quota of jars were replaced on August 14 the poison was added to the bait.

At first the moths were caught at the rate of 80 a night, and the numbers steadily decreased to the end of July when 8 a night were being captured. The third flight of moths commenced while the exposed baits were out, and were caught at the rate of 175 a night when jars were replaced, and the nightly catch declined till, from September 16 onwards, it only averaged 2. A total of 1057 were taken in the second flight, and 1968 in the third flight, while an unknown number were poisoned. Of these 3023 moths approximately 71 per cent. were females, many of them distended with eggs. In order to estimate the effects of this trapping counts of the large conspicuous larvae were made occasionally in one of the end houses, each examination occupying about two hours. On July 23, before the trapping could have affected the numbers of these, 351 were seen, and a week later 150 (reference to Diagram III will show that this reduction was quite abnormal and could not have been obtained by hand-picking). On August 11, 65 were found, and on September 10, 16 only. The larvae following on the large third flight of moths were therefore very few, though in neighbouring blocks where early spraying had been done, those of the third brood could be collected by the thousand in September.

It was thus proved, by methods quite applicable to trade conditions that moth trapping combined with poisoning, is a most useful method of control. The experiment by itself showed that the danger of drawing moths into the houses is negligible, but as there is a confirmed impression that this risk is serious the matter will be discussed a little further. The probable reason why this idea arose is that the growers had no conception of the very large numbers of moths which exist in the infested houses, and so, when they exposed baits, they could account for the numbers trapped in no way except by assuming that moths were being attracted in.

If *Hadena oleracea* was drawn into the houses other common species of moths, which are attracted to these baits, should enter also. Only five individuals, other than this species, were noticed in the traps, and two of these strange moths, *Tryphaena pronuba* and *Xylophasia polyodon*, have been seen in houses where baits were not exposed. One of the baited jars was placed in a tomato house in such a way that it communicated only with the outside, by means of a calico sleeve and wide wire mesh cone. Moths from outside alone could thus get into it (see Pl. X, fig. 6). It was exposed from June 20 to the end of the season, the bait being renewed monthly. Only one moth, a male *H. oleracea*, was taken in it. Finally, even if a few moths were drawn in, they would be trapped or poisoned.

In order to determine how many traps should be used the arrangement in a block of 200-foot houses was varied. In the end house 12 were placed, and in the adjoining houses in succession, 8, 6, 4, 3, 3. They were left for five nights, and after the removal of the moths, were placed in the remaining six houses of the block in the same succession, the end house again receiving 12. After five more nights the moths were again removed and counted. The total numbers caught were as follows:

Number of traps ...	12	8	6	4	3	3
Moths caught ...	47	35	42	22	20	36

The last set of traps communicated on one side with houses in which at this time there were none, and it should be noted that they took less than double the number of moths taken by the three in the next house which were surrounded by other traps. The houses were 22 feet wide, so that the traps would appear to have an effective range of less than 44 feet. Apart from this set of traps, which cannot be used for purposes of comparison, the sets of 12, 8 and 6 were distinctly more effective than the sets of 4 and 3, and the set of 6 had an effect intermediate between those of 12 and 8. In another experiment 3 and 6 traps were exposed alternately in an isolated house for six nights. On the three nights when three were used eight moths were caught, and on three nights when six were exposed the catch was 16. The conclusion drawn from these experiments was that in order to obtain the best results with this bait, jars should be placed every 40 feet down the houses: that is six to each 200-foot house, one at each end, and four others evenly distributed.

The fluid in the jars evaporates slowly in the greenhouses, and the traps remain effective as long as it covers the bottom. In the work just described the depth of the fluid varied from an inch to an inch-and-a-half, and it was found necessary to renew it every third or fourth week. The only attention the traps require during the interval is the occasional removal of the dead moths. These should not be dropped in the houses where they would prove a counter-attraction to the traps, but should be collected in vessels and thrown outside. In mixing the material, one part of treacle by volume should be placed in a vessel with two parts of ale, the exact proportion not mattering, and the mixture should be poured rapidly backwards and forwards from this into another vessel until it runs smoothly. It should then be distributed into the jars and the sodium fluoride added separately to each, as it dissolves very slowly. The amount that can be picked up conveniently on a sixpence (about $\frac{1}{30}$th of an ounce) is required for three fluid ounces.

(iv) DESTRUCTION OF PUPAE.

The picking baskets, especially those lined with sacking, need attention when the season is over, as they harbour pupae. Seven lined baskets were placed in an infested block, and at the end of three weeks were found to contain 24 pupae behind the lining. The practice has been to store these baskets over the winter and to bring them into the houses without attention when the fruit picking begins. The moths then emerge from them and their offspring commence feeding on foliage no longer protected by the early spraying. These baskets should be dipped in boiling water. It was proved by experiment that two seconds immersion is sufficient to kill the pupae, while 30 seconds did not harm the baskets.

Special baskets should always be kept for picking, and those from the market should never be allowed in the houses until they have been treated as described. This applies not only to tomato growing but to all nursery work. There is little doubt but that "red spider," and possibly "white fly" also, may be introduced into a greenhouse with a market basket. Those used for picking should be painted or marked in some characteristic manner so that they may be kept for this purpose alone. If a nurseryman consents to store a salesman's baskets in his glasshouses over the winter he should insist on their being first sterilised by heat.

The canes should be dipped for a few seconds in boiling water to kill any pupae that may be in them.

The houses should if possible be drenched with boiling water before the mulch is removed. Most of the pupae on the ground lie in, or just below, this and if it is taken away untreated some of them will become moths in the following summer. The mulch also contains many wireworms and should not be spread on the fields untreated for this reason also. If the soil is heavy and wet the pupae lie very superficially, but in light dry friable soil they may go to a greater depth. Whenever the soil comes close up to a pipe a spadeful should be dug out from below it and spread thinly over the mulch before the drenching. The grower should inspect his own infested houses and if he finds the pupae at a greater depth than an inch along the walls and around the piers, a spadeful of earth should be removed and spread before the boiling water is used. After this operation a number of pupae should be collected from a variety of positions on the ground and should be placed in a plant-pot on moist earth. After an interval of three or four weeks they should be broken open. If the contents are green and fresh they are still alive and the drenching has been inefficiently done. If the contents are brown and corrupt, or dry, the insects are dead. It is not possible to tell after the brief immersion in hot water whether the pupae are alive or dead unless they are kept some time. Boiling water will be found more effective than carbolic acid for this pest.

Fowls or pigs would scratch up and eat a large number of pupae, and may be allowed in the infested blocks with advantage during the winter.

All crevices and joints in the woodwork should be examined from the ground to the ridge. The old nests of spiders frequently conceal pupae behind them. They are also often found spun up in the angles between the glass and the wood, and are then somewhat inconspicuous. They are often hidden in the wooden ventilators in the walls, and as moths from these would emerge late in the spring, owing to their being kept cool, they should be especially looked for. The stonework should be pointed and lime-washed. It would be a good plan to pass the flame of a painter's blow-lamp into all crevices of the woodwork, especially about the gutter-boards.

(v) General Precautions.

In dealing with this, as with most other pests, it is of great importance that the nurseries should be kept orderly. Weeds should not be allowed to grow either inside or in the neighbourhood of the houses. One reason for this is that the caterpillar can mature so much more quickly upon some of these than on tomatoes. Also, when a man is spraying the plants he is very liable to miss the weeds. Those below the shelves in the propagating houses and stray seedlings should be especially looked for and removed. The border of weeds often allowed to grow around the bases of the walls outside should be constantly hoed up. Caterpillars can easily feed up on those and pass into the houses to pupate.

Fallen broken fruit should never be allowed to lie about in the houses. The moths cannot feed on unbroken fruit but do so eagerly when the skin is ruptured and they can get at the juice. Under experimental conditions moths fed on this diet lived twice as long and laid three times as many eggs as those which were given no food.

6. APPARATUS AND MATERIALS REQUIRED FOR CONTROL.

A spraying machine, knapsack or other type.

A small open boiler for dipping baskets and sacks (a galvanised iron sanitary bin will do well).

Outfit for hot water drenching.

For each acre of tomatoes:
- Sixty jars for moth trapping.
- Arsenate of lead paste, 20 lbs.
- Saponin, 6 ounces.
- Thick treacle, 30 lbs.
- Ale, 48 pints, to be purchased as required.
- Sodium fluoride, 1 lb.

SUMMARY.

H. oleracea is not a normal pest of tomatoes grown under glass, and where it has become established as such it is still in some respects ill adapted to a greenhouse life on a tomato diet. The larvae eat the fruit because many of them are unable to survive on the foliage alone. In spite of this weakness, it has become a serious pest because the species is a prolific one and, once having entered a greenhouse, it usually becomes a prisoner there. In a normal year there are two complete generations and a partial third, and the moths are present in the houses continuously from February to October.

Spraying the young plants with arsenate of lead largely controls the first brood of larvae, but not entirely, because moths of the first flight of the year are still emerging when it is not practicable to use a poisonous spray on the plants. The plants should be sprayed three times when the larvae appear early: (1) when the seedlings are in pots; (2) just after planting out; (3) about a month before fruit picking begins. The last operation is the most important and the two previous ones may be omitted if there are no signs of larvae feeding.

Systematic moth trapping must be done throughout the growing season, because it will reduce the numbers of moths which pass out of the houses, and these, or their offspring blunder into the same or neighbouring greenhouses; and also because it is the most effective form of control when spraying is not practicable, and will reduce the infestation to a very great extent. Sixty jars baited with ale, treacle and 1 per cent. sodium fluoride should be used to each acre of glass. The dead moths should be removed frequently, and the jars should be rebaited every third week.

Broken fruit must not be allowed to lie about in the houses as the moths feed on this and become more prolific.

Many full grown larvae may be trapped in sacks placed about the houses. The sacks should be collected and dipped in boiling water every third week.

Pupae should be destroyed in the winter.

Special baskets should be kept for fruit picking, and those from the markets should never be allowed in the houses.

The pest spreads rapidly through areas where the nurseries are congested owing to the escape of moths from the infested houses. It may be introduced into isolated localities by means of market baskets, or by plants purchased from infested nurseries. On its first appearance every method of control should be applied at once, as attempts to check it by picking off the larvae by hand in trade nurseries have almost invariably ended in failure.

DESCRIPTION OF PLATES

PLATE VIII.

Fig. 1. The damage done to tomato plants by the larvae of *Hadena oleracea*. The shoot is eaten through, the stem is bitten into, and a larva is eating a fruit.

Fig. 2. The larva of *H. oleracea* feeding on the pith of a tomato plant.

PLATE IX.

Fig. 3. Greenhouse screened against invasion by *H. oleracea*.

Fig. 4. Showing the benefits to be obtained by spraying. The plant on the left was sprayed with a suspension of an alcoholic extract of tuba root and then infested with 22 larvae which were all poisoned. The other plant was not sprayed and was infested with 10 larvae which destroyed it in a week.

PLATE X.

Fig. 5. A sack exposed for three weeks in a tomato house infested by *H. oleracea*, showing the trapped pupae.

Fig. 6. Showing a baited trap in a tomato house, communicating only with the outside. In three months only one *H. oleracea* was caught in it. In the same period over 3000 were captured in similar traps in a block of 12 infested tomato houses.

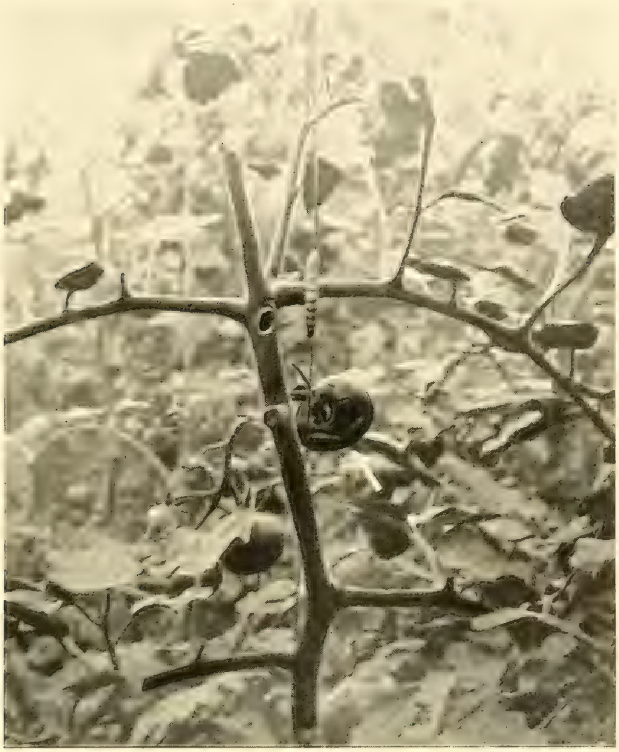

Fig. 1.

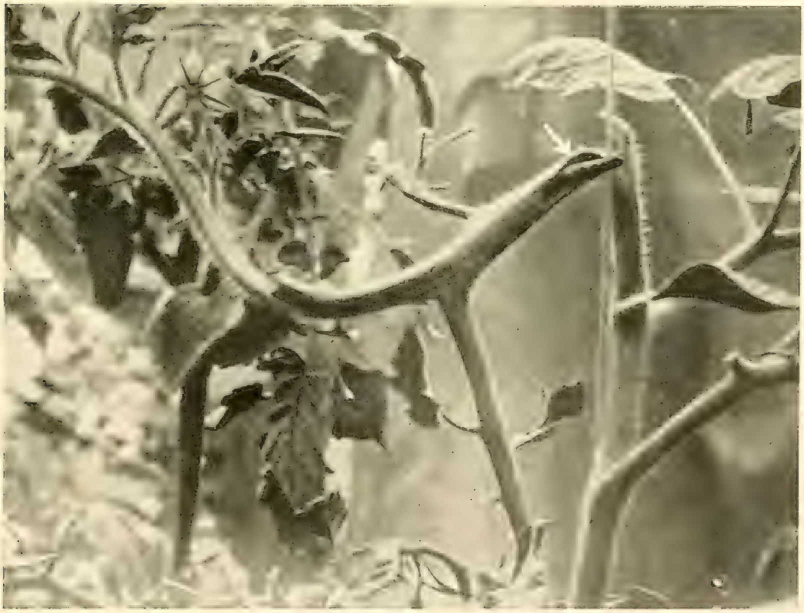

Fig. 2.

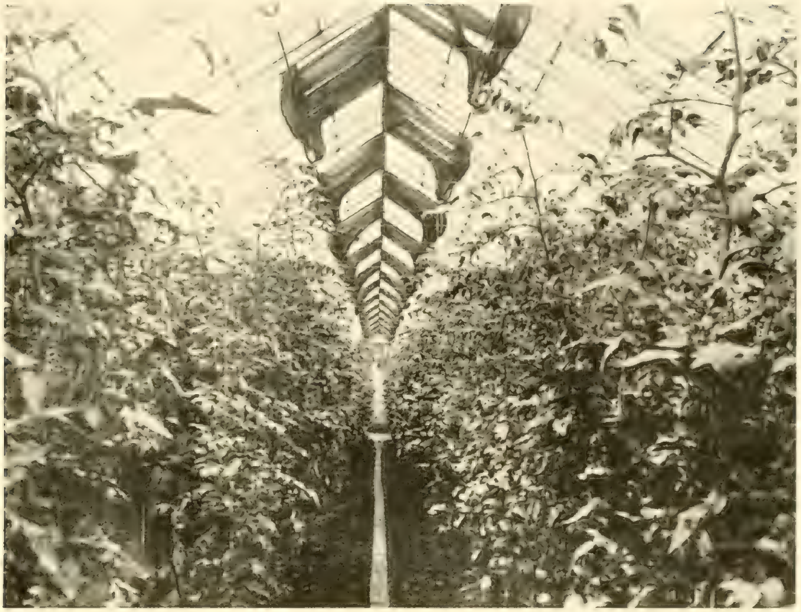

Fig. 3.

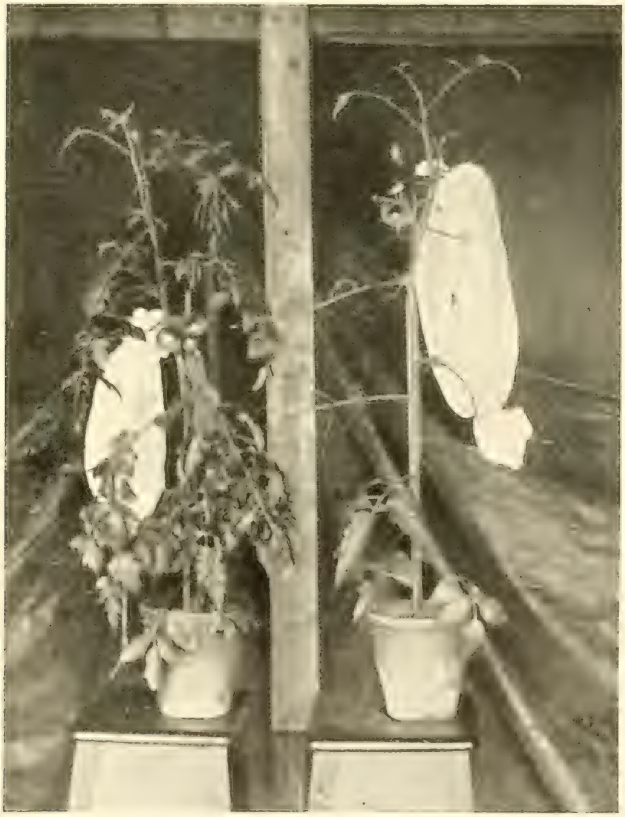

Fig. 4.

Fig. 5.

Fig. 6.

A QUANTITATIVE ANALYSIS OF PLANT GROWTH.

PART I.

By G. E. BRIGGS, M.A. (Cantab.),

FRANKLIN KIDD, M.A. (Cantab.), D.Sc. (Lond.),

AND

CYRIL WEST, A.R.C.Sc., D.Sc. (Lond.).

(With 9 text-figures.)

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Introduction.

The quantitative analysis of plant growth is a branch of plant physiology to which adequate attention has not as yet been paid, but which should be able nevertheless to yield results of much theoretical interest and economic importance. Methods for obtaining data for the analysis of plant growth under ordinary cultural conditions are in general simple, consisting principally of periodic dry-weight and leaf-area measurements, and a quantity of excellent data of this nature has already been collected and exists in the literature. As yet a thorough analysis of these results has not been presented. Attempts have been made to fit in a few isolated results with various empirical laws without wide examination of existing data.

For example it has been recently suggested by V. H. Blackman (1) that the growth of an annual plant can be treated as a process following the compound interest law expressed by the formula

$$W = W_0 e^{rt},$$

where W = the dry-weight of the plant at time t, W_0 = the initial dry weight of the plant, r = the rate of interest or "efficiency index" of dry-weight production, and e = the base of the natural logarithms.

Another suggestion is that the growth of a plant is similar to an autocatalytic reaction, and that it can be expressed by the formula

$$\log \frac{x}{A-x} = K(t-t_1),$$

where A = the maximum dry-weight of the plant, x = the dry-weight of the plant at any time t, t_1 = the time at which the weight of the plant is half the final dry-weight, and K = a constant. This suggestion was put forward by Robertson (24 and 25) and has received the support of Reed and Holland (21) and of Rippel (22 and 23).

Finally Mitscherlich (14, 15 and 16) has attempted to apply to plant growth as measured by dry-weight increase the following formula

$$\log(\sqrt[n]{A} - \sqrt[n]{y}) = \log \sqrt[n]{A} - c \, . \, x.$$

In this formula n = a variable quantity indicating the probable number of environmental factors, A = the maximum possible dry-weight attainable by the plant in question, y = the dry-weight of the plant at time x, the time x being expressed in vegetation periods (Vegetationsabschnitten) of arbitrary length.

A fuller consideration and criticism of these suggestions will be given in subsequent chapters.

In the present paper the primary objective is to attempt to obtain a concrete idea of the growth and development of the plant. At the outset it will be best to confine our attention to simple cases and we propose to devote the first chapter to a consideration of an annual plant.

Certain data are required: periodic dry-weight measurements of the whole plant (and its various parts) at short intervals throughout its life, starting from the seed at the time of sowing; corresponding periodic leaf-area measurements; data with regard to light, temperature, and water supply. To avoid the error due to individual variation, a large number of plants should be used for each dry-weight measurement and where possible uniform 'pure-line' material should be employed.

There are various methods of presenting the results, and in the first instance we shall use the *relative growth-rate curve*. The principle of the proposed method of expressing rate of growth is analogous to that of the method by which the rate of most reactions, both chemical and physiological, are expressed, namely, amount of change per unit of material per unit of time. Since the amount of material in the growing plant is constantly changing, and since the relative rate of growth is not constant, as the following analysis will show, to achieve mathematical accuracy the increase should be measured over an infinitely short period. This procedure is manifestly impossible, and as we have no exact knowledge of the way in which the relative rate of growth varies over a given period we have adopted the following purely conventional method of defining relative rate of growth. The relative rate of growth of a plant during any given week in its life-cycle is the amount of dry matter which 100 g. of dry matter taken at the beginning of the week adds during the week. A week has been chosen since this is the usual interval between determinations of dry-weight in most experiments on growth in plants[1]. It must be realised that the method does not pretend to mathematical accuracy being merely an approximate average for the week, but with such results as are at present available nothing more accurate can be obtained. Even if measurements over

Relative growth-rate curves for "Badischer Früh" Maize, 1876

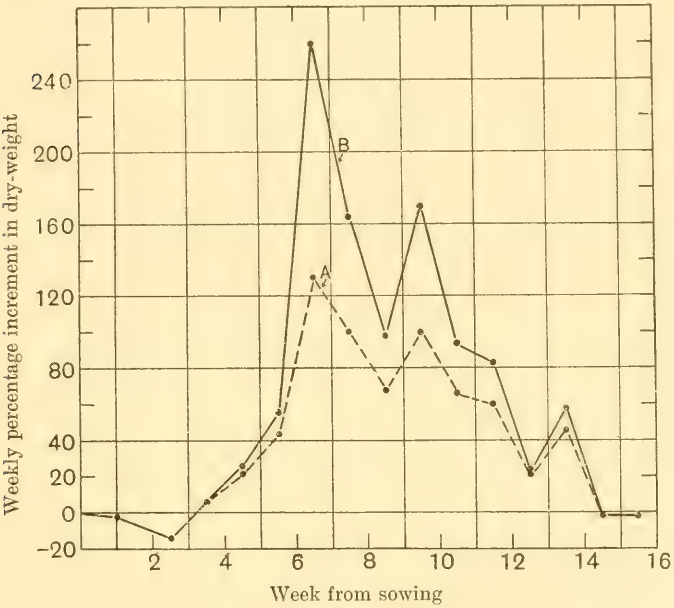

Fig. 1.

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[1] When results are not given for a week we have calculated the increase per 100 g. for the period and divided the result by the number of weeks in the period: for example, if the period is 8 days and 40 g. increases by 20 g. during that period, then the relative rate is $\frac{20 \times 100}{40} \div \frac{8}{7}$.

shorter intervals were available, until we gain knowledge of a mathematical law according to which the rate changes, we cannot determine the rate at any given time.

It might be suggested that allowance could easily be made for the continuous increase in the dry-weight during the week by assuming that this takes place at a uniform rate, and consequently that by means of the following logarithmic formula the rate could be determined:

$$\log W - \log W_0 = r,$$

where W = the dry-weight at the end of the week, and W_0 = the dry-weight at the beginning of the week.

In curve A, Fig. 1, this allowance has been made. In Curve B the ordinates are relative growth-rates calculated by our method, that is, without making allowance for the continuous increase during the week. These curves show similar variations in relative rate from week to week. The more complicated method, however, does not achieve accuracy as it rests on the assumption that the rate remains constant during the week, an assumption manifestly incorrect since the rate varies from week to week. Both methods are purely conventional and only approximate to accuracy, and nothing definite is to be gained by adopting the more complicated procedure.

The relative rate of plant growth at any time may be taken as an expression of the efficiency of the plant at that time in producing dry matter. It must be remembered from what we have said above that the actual value of the figures for the growth-rate is only an average of the changing rate during a week. They are, however, valid for purposes of comparing the rate of a plant's growth from week to week.

The gist of the method described above of presenting the results of growth experiments has been previously briefly put forward by Kidd and West (9).

CHAPTER I.

THE RELATIVE GROWTH-RATE CURVE FOR MAIZE.

The most complete set of data for one plant is to be found in a series of papers published in Germany many years ago under the general direction of U. Kreusler (10, 11, and 13). From among the many results recorded, we have chosen those for maize, since the growth of this plant was studied in four successive years. The data include not only weekly dry-weight measurements and corresponding leaf-area measurements, but also environmental conditions such as light, temperature, water-supply, etc. The dates of the first appearance of the flowers and of seed formation are also given. The work appears to have been carried out without any pre-conceived idea as to what the results would be, and the results themselves have not as yet been worked out nor have they received critical consideration although collected and published 40 years ago. These results will be analysed in this and in the following chapter, and certain interesting conclusions reached. We have constructed from Kreusler's data the tables and figures presented in this paper. Figs. 2 and 3 show respectively the relative growth-rate curves for "Badischer Früh" maize, the rates being calculated, as above described, on the basis of weekly periods for the years 1875–1878 inclusive, and for five different varieties of maize calculated on the same basis for the year 1875.

Table I.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·206						
1st June	21	0·268	0·062	(30)* 10	33·3	124	14	
8th ,,	7	0·559	0·291	108	97·8	177	19·3	
15th ,,	7	1·069	0·510	91	181·1	170	17·1	
23rd ,,	8	2·448	1·379	(129) 113	405·1	167	16·6	
30th ,,	7	4·776	2·328	95	889	186	17·0	
7th July	7	11·077	6·301	132	1543	139	19·9	♂ flowers
13th ,,	6	23·619	12·542	(113) 132	2646	112	18·1	♀ flowers
21st ,,	8	43·844	20·225	(85) 74	3633	83	18·8	
27th ,,	6	55·934	12·090	(28) 33	3291	59	17·6	
3rd Aug.	7	72·875	16·941	30	3617	50	16·9	
10th ,,	7	76·619	3·744	5	3630	48·5	19·1	
17th ,,	7	84·332	7·713	10	2933	34·5	21·5	
24th ,,	7	89·621	5·289	6	2696	30	19·8	
31st ,,	7	100·380	10·759	12	2907	29	19·0	
7th Sept.	7	130·478	30·098	30	2986	23	16·1	
15th ,,	8	158·139	27·661	(21) 18	2335	14·8	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table II.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1876.

Date of harvest 1876	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Number of hours of sunshine	Mean temperature for the week °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·3264							
				(−2·91)*					
24th ,,	13	0·3169	−0·0095	−1·57				9·8	
31st ,,	7	0·2724	−0·0445	−14	8·4	31	42	13	
7th June	7	0·2914	+0·0190	+ 7	19·0	65	61	15·1	
14th ,,	7	0·3642	0·0728	25	41·4	113	16	16·3	
21st ,,	7	0·5674	0·2032	56	92·0	162	57	16·9	
28th ,,	7	2·0733	1·5059	260	350·8	170	102	19	
5th July	7	5·655	3·582	164	987·0	172	42	17·6	
12th ,,	7	11·151	5·496	97	1794·5	159	45	20	
19th ,,	7	30·265	19·114	170	3272·6	108	71	17·6	♂ and ♀
26th ,,	7	58·609	28·344	93	4959·8	85	49	18·5	flowers
2nd Aug.	7	106·908	48·299	83	6196·7	58	93	20·3	
9th ,,	7	131·169	24·261	22·7	5530·7	42	76	18·3	
16th ,,	7	207·373	76·204	58·2	6666·7	32	94	21·9	
23rd ,,	7	204·436	−2·937	−1·42	6201·4	30·5	77	21·6	
30th ,,	7	202·168	−2·268	−1·12	4231·4	21	10	14·5	

* The figure in brackets in column 5 gives the percentage increase in dry-weight for 13 days.

Table III.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1877.

Date of harvest 1877	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Number of hours of sunshine	Mean temperature for the week °C.	Record of appearance of ♂ and ♀ flowers
17th May		0·3353							
				(−3·88)*					
29th ,,	12	0·3223	−0·013	− 1·9			14	11·9	
5th June	7	0·2819	−0·404	−12·6	5·43	19·2	44	16·6	
12th ,,	7	0·2877	+0·0058	+ 2·13	45·7	159	33	19·1	
19th ,,	7	0·9395	0·6518	227	168·8	180	54	18·7	
26th ,,	7	2·500	1·650	176	477·5	192	32	18·8	
3rd July	7	6·365	3·775	150	1060	166	40	18·0	
10th ,,	7	10·637	4·272	67	1671	157	20	14·7	
17th ,,	7	24·447	13·810	130	3216	132	27	19·0	♂ flowers
24th ,,	7	41·408	16·961	69	3788	92	38	17·5	♀ flowers
31st ,,	7	66·498	25·09	61	4591	69	20	18·6	
7th Aug.	7	88·654	22·156	33·4	4934	55·5	40	16·4	
14th ,,	7	119·842	31·188	35	5298	44	19	19·3	
21st ,,	7	135·532	15·690	13	4852	35·5	30	19·5	
28th ,,	7	140·782	5·250	3·9	4158	29·5	17	18·1	
4th Sept.	7	179·973	39·191	28	4332	23	25	16·6	
11th ,,	7	187·795	7·822	4·35	4035	21·5	17	13·0	
18th ,,	7	201·293	13·498	7·2			18	16·0	
25th ,,	7	220·709	19·416	9·4			9	9·7	
2nd Oct.	7	199·970	−20·739	−9·4			22	7·9	
9th ,,	7	204·017	+4·047	+2·0			9	9·0	

* The figure in brackets in column 5 gives the percentage increase in dry-weight for 12 days.

Table IV.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1878.

Date of harvest 1878	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Number of hours of sunshine	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
20th May		0·3282							
28th ,,	8	0·3280	−0·0002					12·4	
4th June	7	0·2870	−0·041	−12·5			40	13·6	
11th ,,	7	0·2550	−0·032	−11·2	17·9	70	27	15·5	
18th ,,	7	0·3080	+0·053	+20·8	29·2	95	19	15·1	
25th ,,	7	0·6370	0·329	106·5	124·4	195	40	17·9	
2nd July	7	2·319	1·682	264	419·2	181	36	19·8	
9th ,,	7	4·654	2·335	100	762·2	174	16	17·1	
16th ,,	7	9·019	4·365	94	1301	144	20	16·8	
23rd ,,	7	20·001	10·982	122	2136	107	57	19·6	♂ and ♀
30th ,,	7	34·557	14·556	72	2805	81	23	19·8	flowers
6th Aug.	7	57·587	23·030	66	3384	59	35	18·2	
13th ,,	7	70·095	12·058	21·7	3047	43·5	32	20·1	
20th ,,	7	85·165	15·070	21·4	3025	35·5	35	19·3	
27th ,,	7	111·649	26·484	31	2976	26·5	17	17·8	
3rd Sept.	7	124·760	13·111	11·7	2684	21·5	21	19·0	
10th ,,	7	121·990	−2·770	−2·2	2387	19·5	35	19·2	

Table V.—"*Hühner*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq.cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·127						
1st June	21	0·149	·022	(17)* 5·7	28·9	194	14·0	
8th ,,	7	0·476	·327	220	86·3	181	19·3	
15th ,,	7	0·824	·348	73	153	186	17·1	
23rd ,,	8	1·765	·941	(114) 100	371	210	16·6	
30th ,,	7	2·847	1·082	61	627	220	17·0	
7th July	7	7·292	4·445	156	895	123	19·9	♂ and ♀ flowers
13th ,,	6	11·570	4·278	(59) 69	749	65	18·1	
21st ,,	8	21·576	10·006	(86) 75	1416	66	18·8	
27th ,,	6	40·735	19·159	(89) 104	2126	52	17·6	
3rd Aug.	7	55·918	15·183	37	1917	34	16·9	
10th ,,	7	60·648	4·730	8·5	2196	36	19·1	
17th ,,	7	73·946	13·298	22	2254	31	21·5	
24th ,,	7	90·491	16·545	22	2090	23	19·8	
31st ,,	7	88·212	−2·279	−2·5	2032	23	19·0	
7th Sept.	7	81·618	−6·594	−7·5	1367	17	16·1	
15th ,,	8	76·385	−5·233	(−6·4) −5·6	665	9	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table VI.—"*Oberländer*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·107						
1st June	21	0·162	0·055	(51)* 17	31	192	14·0	
8th ,,	7	0·467	0·304	188	96·7	207	19·3	
15th ,,	7	0·955	0·488	105	165·3	173	17·1	
23rd ,,	8	1·839	0·884	(89) 78	374·1	203	16·6	
30th ,,	7	3·097	1·258	67	621·0	201	17·0	
7th July	7	6·758	3·661	118	668·6	99	19·9	♂ and ♀ flowers
13th ,,	6	14·448	7·690	(114) 133	950·6	66	18·1	
21st ,,	8	24·890	10·442	(72) 63	1098	44	18·8	
27th ,,	6	30·180	5·290	(21) 25	1407	47	17·6	
3rd Aug.	7	51·196	21·016	70	1653	32	16·9	
10th ,,	7	70·978	19·782	39	2217	31	19·1	
17th ,,	7	59·110	−11·868	−17	2359	40	21·5	
24th ,,	7	81·687	22·577	38	1464	18	19·8	
31st ,,	7	73·921	−7·766	−9	1235	16	19·0	
7th Sept.	7	74·120	0·199	0·3	1716	10	16·1	
15th ,,	8	87·192	13·072	(18) 15	514	6	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table VII.—"*Ungarischer Früh*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·2696						
1st June	21	0·2672	−0·0024	(−0·88)* −0·29	31·0	116	14·0	
8th ,,	7	0·609	0·342	128	118·9	196	19·3	
15th ,,	7	1·110	0·501	82	190·2	172	17·1	
23rd ,,	8	2·143	1·033	(93) 81	393·2	184	16·6	
30th ,,	7	4·123	1·980	93	807·0	196	17·0	
7th July	7	12·101	7·978	195	2109	174	19·9	♂ and ♀ flowers
13th ,,	6	23·244	11·143	(92) 107	3030	130	18·1	
21st ,,	8	44·48	21·236	(91) 80	4329	97	18·8	
27th ,,	6	70·46	25·98	65	5635	80	17·6	
3rd Aug.	7	104·98	34·52	49	8827	58	16·9	
10th ,,	7	92·85	−12·13	−12	4975	54	19·1	
17th ,,	7	121·78	28·93	30	4894	40	21·5	
24th ,,	7	169·53	47·75	38	3454	20	19·8	
31st ,,	7	212·72	43·19	25	4807	23	19·0	
7th Sept.	7	213·29	0·57	0·3	5204	24	16·1	
15th ,,	8	202·19	−11·10	(−5) −4	2738	14	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table VIII.—“*Pferdezahn*” *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·294						
1st June	21	0·286	−0·010	(−3·4)* −1·1	36·2	126	14·0	
8th ,,	7	0·517	0·232	80	77·9	150	19·3	
15th ,,	7	1·023	0·506	98	177	174	17·1	
23rd ,,	8	1·781	0·758	(74) 65	335	188	16·6	
30th ,,	7	3·826	2·045	115	730	190	17·0	
7th July	7	9·064	5·238	135	1686	187	19·9	
13th ,,	6	17·292	8·228	(91) 106	2578	149	18·1	
21st ,,	8	29·704	12·41	(72) 63	3984	134	18·8	
27th ,,	6	54·998	25·29	(85) 100	6274	114	17·6	
3rd Aug.	7	73·949	18·95	32	6622	90	16·9	
10th ,,	7	108·68	34·73	46	8453	77	19·1	♂ and ♀
17th ,,	7	153·61	45·93	41	8823	57	21·5	flowers
24th ,,	7	173·18	18·57	12	8258	48	19·8	
31st ,,	7	210·37	37·19	21	7090	34	19·0	
7th Sept.	7	245·09	34·72	(−16·5) −14·5	9200	38	16·1	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

In forming a clear picture of the growth of the plant as presented by its increase in dry-weight, it is as well to keep in mind the fact that from 80 % to 90 % of the dry-weight is the result of the process known as carbon-assimilation and that the actual percentage of the dry-weight of the plant derived from the mineral constituents of the soil is relatively small (cf. Hornberger(6), Monnier(17), Rabinovitch(20) and others(26, 4, 8 & 3))[1].

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[1] Jones and Huston(8) give the following figures for the ash of maize at different periods:

Date of sampling (week from sowing)	Ash (percentage of the total dry-weight of the plant)
3rd	12·0
9th	12·2
11th	8·7
14th	6·0
16th	5·3
18th	4·8
19th	4·1
20th	4·1

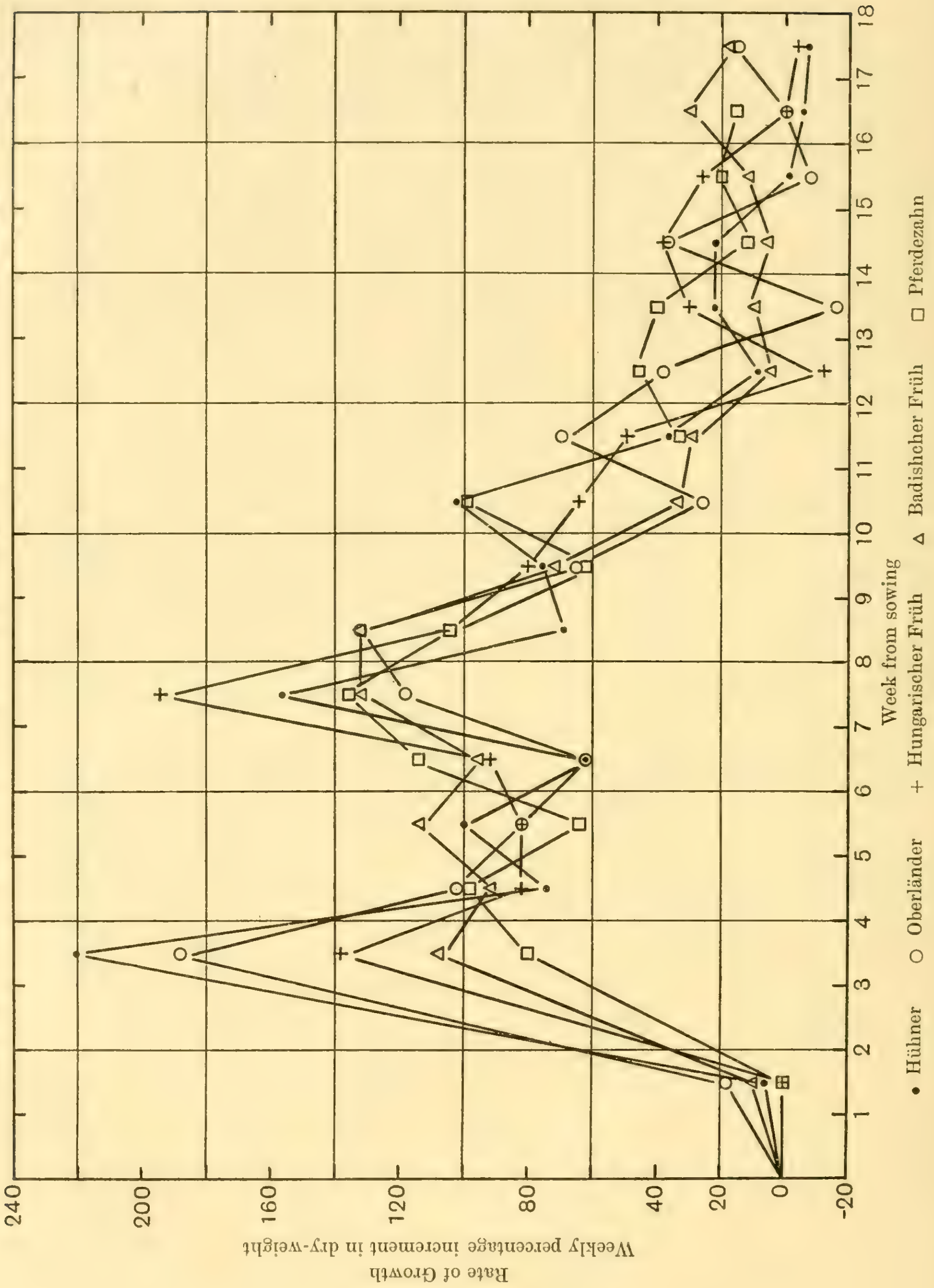

Fig. 2. Relative growth-rate curves for five varieties of maize grown at Poppelsdorf in the year 1875.

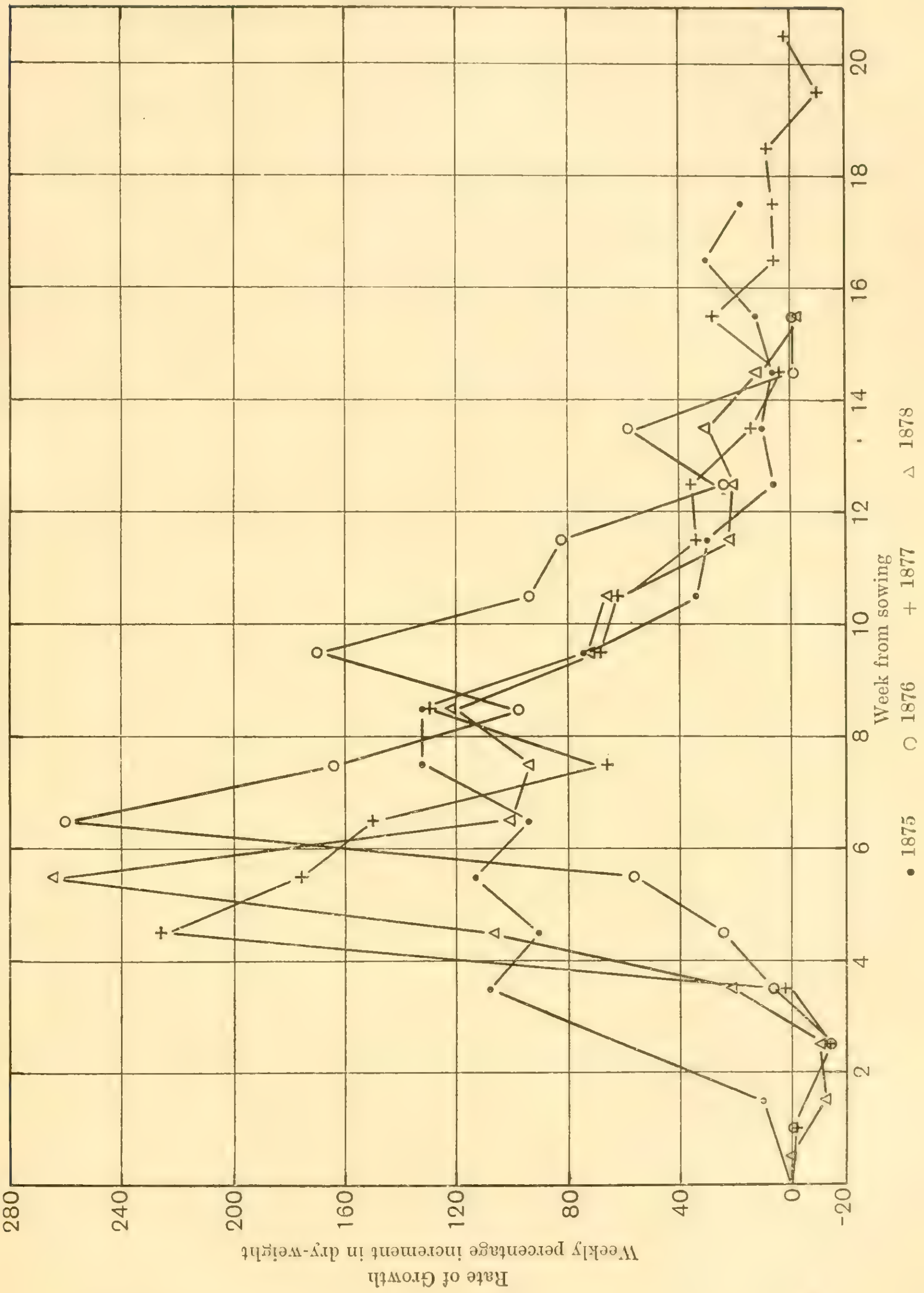

Fig. 3. Relative growth-rate curves for "Badischer Früh" maize in four successive years.

It follows that the relative rate of growth at any time is almost the same as the difference between the rates of assimilation and respiration per 100 g. dry-weight at that time.

We will now proceed to consider the curves. In following the curves in Fig. 3 from the date of sowing, there is seen to be an initial phase lasting for about three weeks during which the rate of growth is negative, in other words, the plant is actually losing in weight[1]. This phase of negative growth persists until a point in the development of the plant is reached at which approximately four leaves have appeared. During the time occupied by germination, before the appearance of these leaves, the negative rate of growth is clearly to be attributed to a loss of carbohydrate through respiration. The order of magnitude of the loss in dry-weight through respiration in germinating seeds is 3 % to 6 % of their dry-weight per day at 16° C. (Garreau (5)). In the latter part of the period, where, despite the fact that the plant possesses from 1–4 leaves, the negative rate of growth persists, it is obvious that any increase in dry-weight due to assimilation is more than counter-balanced by a loss in weight through respiration. Evidence obtained by an analysis of Kreusler's data as to whether the leaves at this stage perform their normal assimilatory function, or not, will be considered shortly. After this initial phase there ensues a short period varying from 1–4 weeks during which the rate of increase in dry-weight rises rapidly to its maximum value, followed by a long period constituting the remainder, and larger part, of the life-cycle of the plant, throughout which the rate of growth falls off more or less continuously. This falling part of the curve, however, shows subsidiary maxima.

The question arises of what kind of change in the plant this perfectly definite type of curve in the main period of growth is an expression. It is clear that this main rise and fall must be due to an increasing difference between the rate of assimilation and the rate of respiration per unit dry-weight in the first phase and to a decreasing difference in the second phase. The order of magnitude of respiration in terms of dry matter consumed per week during the main growth period of the plant is probably not greater than 20 %–40 %, which is the order of magnitude of the loss in dry-weight through respiration during germination. As against this the actual percentage increase in dry-weight per week varies from 0 % to over 200 %, this being the balance when loss due to respiration is subtracted from gain due to assimilation, etc. Consequently it is obvious that changes in the rate of respiration per unit dry-weight of sufficient magnitude to affect the rate of growth to the extent observed are inconceivable. We must turn therefore to the changes in the rate of assimilation per unit dry-weight in order to account for the main rise and fall which characterises the growth-rate curve. Brief consideration will show that the rate of assimilation per unit dry-weight is most probably a function of the amount of leaf-area per unit dry-weight mainly, and it is interesting to enquire therefore to what extent changes in leaf-area per unit dry-weight correspond with those in the rate of growth. The values of the ratio of leaf-area to dry-weight throughout the life-cycle of the plant can be calculated from Kreusler's data, and when these values are plotted against time there appears a striking similarity between this curve and the growth-rate curve (see Figs. 4, 5, 6 and 7).

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[1] In the year 1875 the first dry-weight measurement was not taken until the end of the third week. The average plotted in Fig. 3 gives no indication of the variations in the individual weekly growth-rates.

From this we may conclude, therefore, that the main rise and fall shown by the growth-rate curve is merely an expression of the rise and fall in the ratio of leaf-area to dry-weight.

To return to the question of the assimilation of the young leaves on their first appearance, an inspection of Figs. 4, 5, 6 and 7 will show that at this stage the ratio of the ordinate of the growth-rate to that of the leaf-area curve (which ratio is really a measure of the increase in dry-weight *per unit leaf-area*) is a negative or very small quantity compared with the ratio during the main period of high relative rate of growth. This fact strongly suggests that the assimilatory power of the young leaves for some time after their first appearance is negligibly small. It is interesting to find that this inference which is drawn from an analysis of plant growth, as presented in this paper, is corroborated by direct experimentation on the assimilatory power of young leaves (Irving (7) and Briggs (2))[1].

Another point of interest which arises from a comparison of the leaf-area ratio with the growth-rate curve is that, while the growth-rate curve exhibits one or more subsidiary maxima in the falling phase, the leaf-area ratio curve on the other hand falls uninterruptedly.

With regard to these subsidiary maxima exhibited by the growth-rate curve there is a significant correlation between the times of their occurrence and the recorded times of the first appearance of the male and female flowers (see Figs. 4–8). Results obtained with maize by Morgen (18) and Osswald (19) who worked in conjunction with Kreusler,

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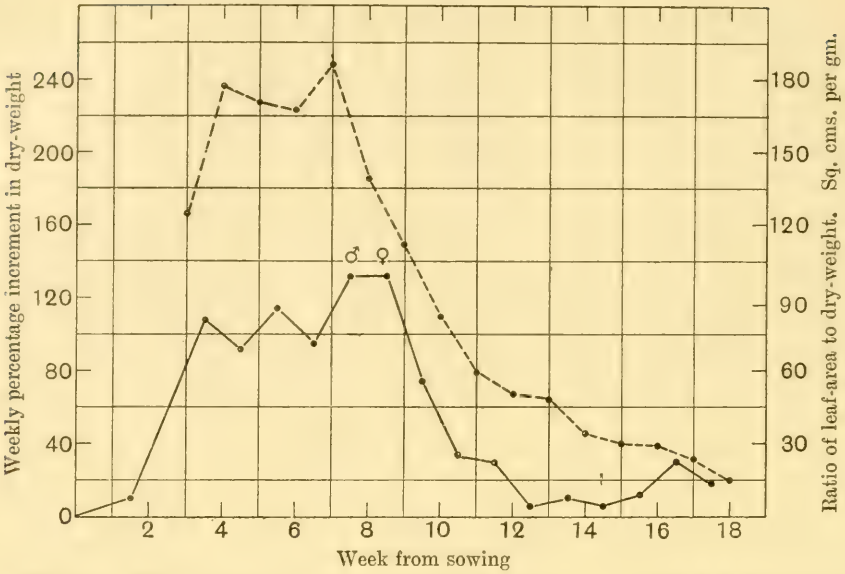
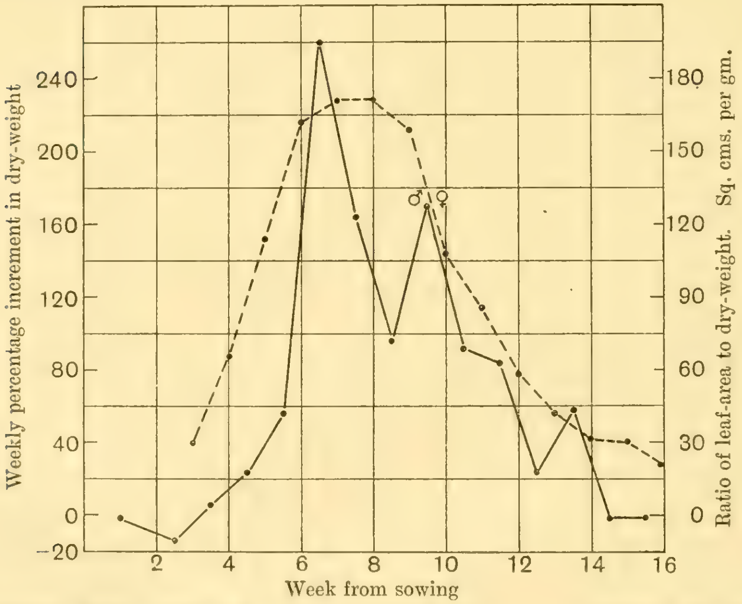
[1] Also unpublished results for maize.



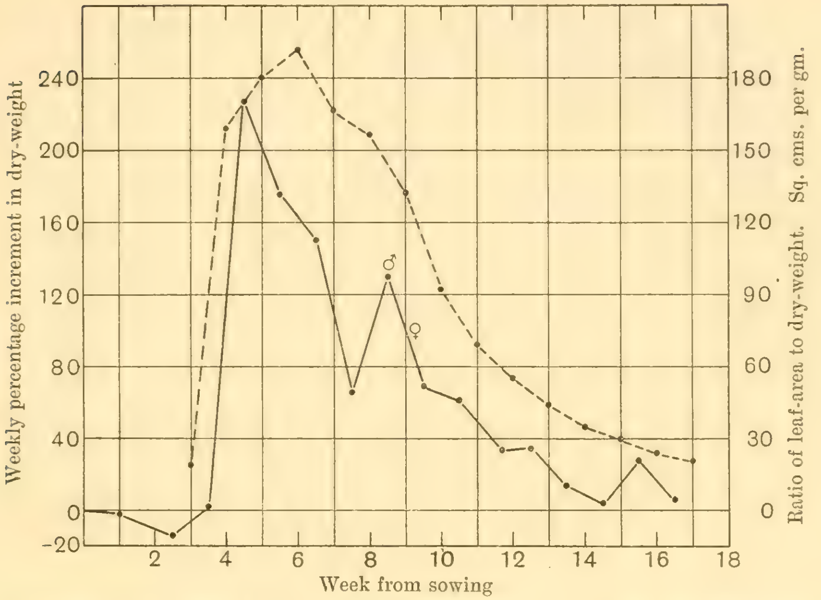
"Badischer Früh" maize 1875 ——— Growth curve ...... Leaf-area ratio curve

Fig. 4.



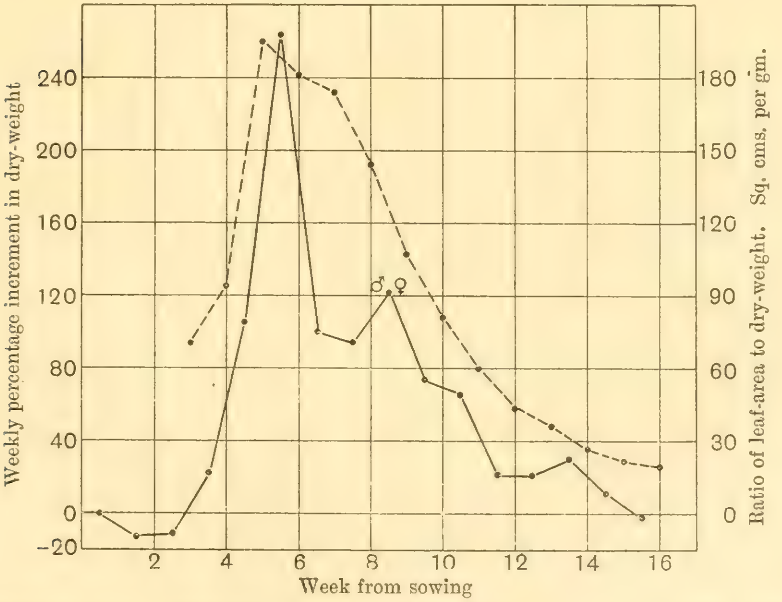
"Badischer Früh" maize 1876 ——— Growth curve ...... Leaf-area ratio curve

Fig. 5.



"Badischer Früh" maize 1877 ——— Growth curve ...... Leaf-area ratio curve

Fig. 6.



"Badischer Früh" maize 1878 ——— Growth curve ..... Leaf-area ratio curve

Fig. 7.

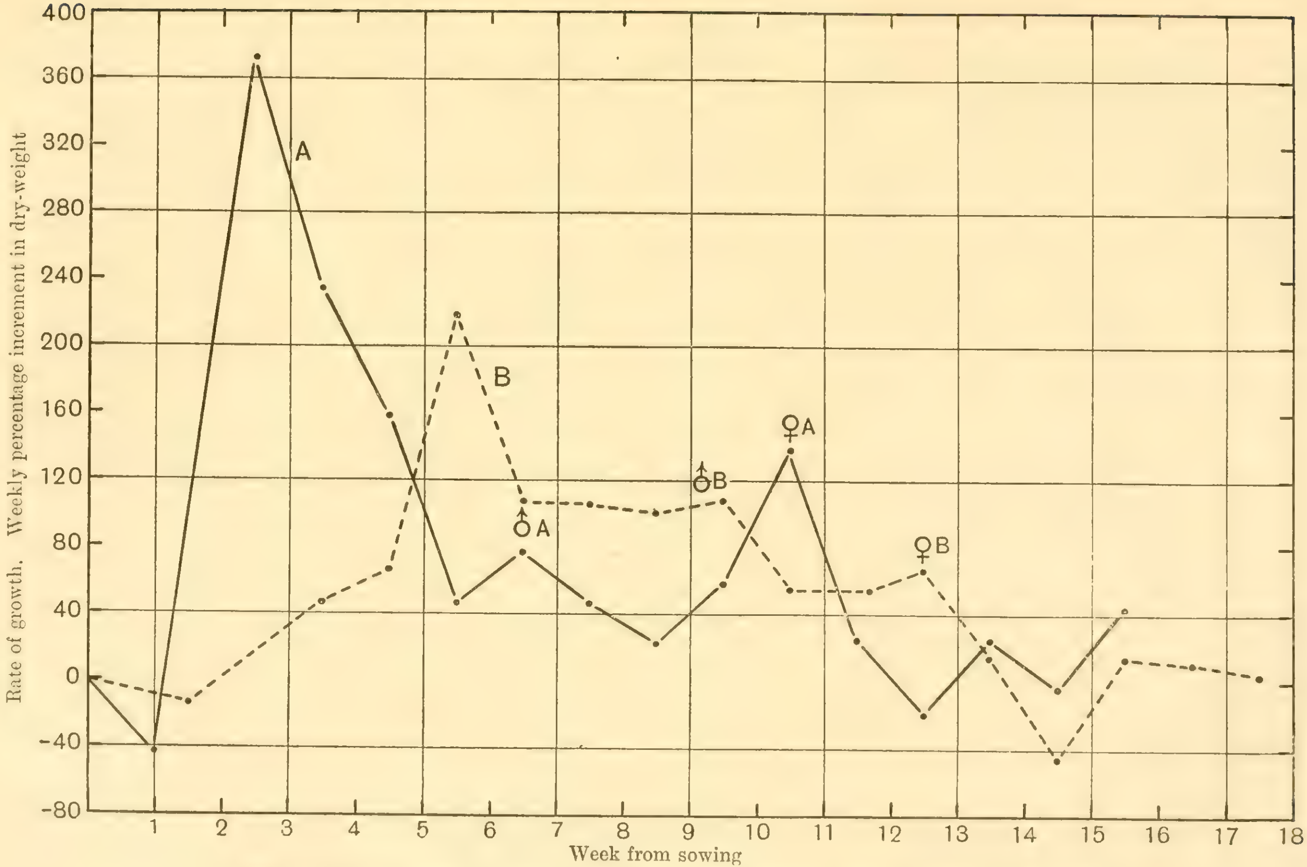
are given in Fig. 8. These results are for tops only, not for the entire plant, including roots, as in the other cases.

It is striking that when there is only one prominent subsidiary maximum the male and female flowers appear together. These subsidiary maxima cannot be correlated with recorded variations in any climatic conditions and consequently it seems safe to conclude that they must be due to internal changes.

In endeavouring to explain these maxima and their correlation with the appearance of the male and female flowers in terms of assimilation and respiration there are two alternatives. The first is to suppose that at the recorded time of the appearance of the flowers there is a temporary increase in assimilation per unit leaf-area or a decrease in respiration per unit dry-weight, or a temporary increase in salt absorption by the roots. The other alternative is to suppose that during the early stages of flower development, prior to the first record, the reverse conditions obtain, in other words, that the minima immediately preceding the record of the appearance of flowers is to be attributed to these reverse conditions. Since it is a well-known fact that flower development is accompanied by an increased respiratory activity and also since we have no evidence that there is an alteration in assimilation per unit leaf-area connected with flower-formation, the safest conclusion at present seems to be that the minima are to be correlated with increased respiratory activity at these periods.

Plants grown at the same time under similar conditions show a coincidence of the maxima (Fig. 2), but when we compare plants grown at different times and under different conditions the incidence of the maxima varies (Fig. 3). It appears likely therefore that the incidence of the maxima depends upon external conditions. As attempts to correlate the maxima with the environmental conditions obtaining at the time of their incidence were unsuccessful, we have concluded that most probably the time of the incidence of the maxima is determined by environmental conditions obtaining at previous stages in the plant's development.

Having now considered the whole of the growth-rate curve for maize it appears on the basis of the data available that the general form of the curve and the occurrence of its various maxima are controlled by internal changes intercorrelated with morphological developments. The points in morphological development which appear to be significant are (1) the rise to a maximum and the subsequent fall in the leaf-area dry-weight ratio, (2) the development of the male flowers, and (3) the development of the female flowers. Environmental conditions may influence



A. "Badischer Früh" maize (Morgen). B. "Italienische Bastard" maize (Osswald). *Tops only.*

Fig. 8.

the time relation of these points and thus the time relations of the maxima on the curve. In extreme cases the environmental factors may so far affect morphological differentiation as to cause coincidence of the maxima.

External conditions, in addition to causing modification in this way in the general form of the growth-rate curve, must directly affect the absolute value of the growth-rate, but an analysis of these curves and attempts to correlate still smaller fluctuations in these curves from year to year with external conditions have not yielded any definite results. We shall return to the subject of the effect of external conditions when dealing later with another form of expressing growth-rate, namely increase in dry-weight per unit leaf-area per unit time.

In a future chapter we propose to compare the relative growth-rate curves of other annual plants with those for maize which have been dealt with above.

Average Growth-Rate.

A full consideration of all the data presented here will show the extraordinary difficulty of finding any valid basis for comparing plants such as maize by means of their average growth-rate whether the average is taken over the whole life-cycle, which is of varying length, or whether arbitrary periods of shorter duration are taken. It is particularly misleading to compare the average growth-rate for one period of one plant with a different period of another plant. For example, a comparison of any two plants by means of their average growth-rate over a period such as six weeks would be favourable to one, whereas a comparison over say 12 weeks might be favourable to the other.

In a subsequent chapter dealing with the question of growth-rate in relation to yield, this point will receive detailed consideration.

Summary.

The series of articles of which this is the first instalment, constitutes an attempt to formulate methods for the quantitative analysis of plant growth and to apply these methods to data which have been lying dormant in the literature for 40 years.

In the present chapter the relative growth-rate curve, which is the weekly percentage increase in dry-weight plotted against time, and also the leaf-area ratio curve, that is, the leaf-area in sq. cms. per g. plotted against time, have been employed. And as a typical example of an annual plant maize has been selected since data are given by Kreusler for this plant grown in four successive years.

The first noteworthy result of this analysis is the demonstration of the fact that the growth-rate varies greatly in magnitude at different periods in the life-cycle of a plant such as maize in a perfectly definite manner.

Fig. 9 gives the generalised form of the growth-rate curve for maize throughout its life-cycle. Although the broad form is that of a Sach's grand period curve, it must be noted that it is not a grand period curve, since the grand period curve as defined by Sachs is the curve of the actual increment per unit of time plotted against time and not of relative increment, that is, increment per unit of matter per unit of time plotted against time. On the broad form of the relative growth-rate curve for maize are superposed three secondary features, an initial fall, and two subsidiary maxima on the descending limb.

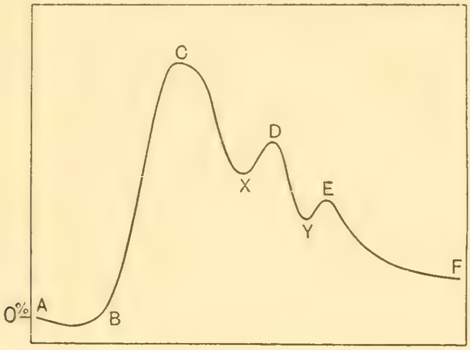


Fig. 9. Generalised form of the growth-rate curve for maize.

In this generalised curve the initial period A–B is the period before the assimilatory organs are able to counterbalance the loss in dry-weight due to respiration, and the rate of growth is consequently negative or nil. The phase B–C corresponds to a phase in morphological development during which the leaf-area per unit dry-weight increases to a maximum. The phase C–F covers the remainder of the life-cycle of the plant during which the leaf-area per unit dry-weight is continuously decreasing. The subsidiary maxima D and E coincide with the time of the record of the appearance of the male and female flowers respectively. The minima X, Y which precede these maxima, correspond with the earliest stages of flower development, and are possibly due to increased respiration during that period.

The incidence of the maxima is controlled by environmental conditions—not by the environmental conditions operating at the time, but by those obtaining at some previous stage in the life-history of the plant.

The fact that the curve for leaf-area per unit dry-weight throughout the season (which has been calculated) shows a correspondence with the growth-rate curve indicates that the physiological basis for increased and decreased relative rate of growth is a corresponding change in the assimilating area per unit dry-weight. This point will be dealt with in the next chapter.

Evidence from the quantitative analysis of plant growth for maize indicates that the seedling leaves do not perform their normal assimilatory function till some time after their appearance.

(*To be continued.*)

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NOTES ON CHEMOTROPISM IN THE HOUSE-FLY.

By E. R. SPEYER.

The experiments described in this paper were carried out under the auspices of the Bureau of Entomology, United States Department of Agriculture, at Washington in 1914.

Acknowledgments are due to the Bureau for permission to publish these notes, and to Dr L. O. Howard, Mr W. D. Hunter, to the Bureau of Chemistry and the Institute of Chemical Research, for much valuable assistance in making the records.

In its original form, this paper embodied a Synopsis and Review of literature upon Chemotropism in Insects up to the year 1914, but it has been decided to omit these, in view of the existence of at least one publication dealing with the literature, and of other important work done by Entomologists since these notes were written.

It may be explained here that the terms Positive and Negative Chemotropism are applied respectively to substances which exert a definite attraction and a definite repulsion to the insects mentioned.

SECTION I.

PRELIMINARY EXPERIMENTS UPON THE ATTRACTION OF THE HOUSE-FLY BY COMMON FOOD-STUFFS.

(*a*) *Type of trap used.*

In all these and future experiments here described, the No. 1 Galvanized "Perfect" Fly-Trap (to be obtained from the Ludlow-Saylor Wire Co., St Louis, Missouri) was employed. It is about 2 feet 6 inches high, 8 inches in diameter at base, composed of wire gauze supported by three metal strips, and fitted with a metal lid. At the base of the trap is an inverted wire cone with a rim of supporting metal. This rim fits closely within a corresponding ring on the outside wire, to which it can be fixed by means of three screws. At the top of the cone is a small hole which admits the insects into the trap. The bait is placed in a dish beneath the wire cone.

(*b*) *Collection of insects from the traps.*

After an experiment the insects contained in the traps were killed by the emersion of the whole trap in hydrocyanic acid gas, generated from potassium cyanide and sulphuric acid (dil.) in a small crucible placed at the bottom of a large metal vessel, used generally for the removal of manure from stables. After about two minutes exposure the insects were shaken on to a sheet of paper and collected in glass vials.

Special note was taken of any flies found dead in the traps (by careful removal of the cone) before exposure to the gas, and also of insects found dead in the bait-dishes.

(*c*) *Disposition of traps.*

In these preliminary experiments, six traps were placed upon the floor of a stable at the Government Agricultural Experiment Station near Arlington, Washington D. C., U.S.A.

In this stable were two horse-boxes where large numbers of house-flies were breeding. Six traps, A, B, C, D, E and F were used for the experiments, located as follows:—The distance between A and B, C and D, E and F, in each case was 6 inches, the distance between B and C, D and E was 10 feet respectively, and the distance from F to A 15 feet. Traps B, C and E had, for baits, various attractive substances, whilst A, D and F had, in the first series of experiments, a control substance—the same in each trap—of moderate attractive power: in the second series a control substance of great attractive power.

After a convenient interval, the traps B, C and E were interposed with their baits, so that they occupied each position for three equal periods of time, and the contents of each trap in its three positions were added together.

(*d*) *Sources of error and their compensation.*

1. Owing to the nature of the traps, a number of flies might escape from the entrance to the trap, after being attracted to a specific substance, and fly to another trap.

All the traps in an experiment would be affected to a similar degree, so that the error is of little magnitude.

2. The position of some traps was certainly more favourable than that of others, apart from the power of the attractive substances used in them.

This was fully compensated for by the interposition of the traps described under (*c*).

3. A different temperature over any one period of time from that of another would have the effect of influencing the number of flies attracted to traps placed in the most favourable positions.

This error, which could not be rectified, is the only one to be considered, and it is very unlikely that the figures given were affected to anything but a negligible degree.

Experiment 1. *Common food-stuffs.*

Date:—August 27th–29th.
General weather conditions:—Dull, cool at start.
Bright, hot at finish.
Duration of experiment:—90 hours.

Exp.	Substance	Amount	Flies caught ♂	♀	Total	Control substance	Flies caught ♂	♀	Total
1	Banana	½ crushed in dish	456	715	1171*	Brown sugar and water	20	25	45
2	Vanilla extract in 61 % alcohol	30 c.c.	111	229	340†	,, ,,	8	9	17
3	Acetic acid (glacial)	30 c.c.	2	4	6	,, ,,	1	10	11

* Includes 147 ♂♂ and 204 ♀♀ found dead in traps.

† Includes 15 ♂♂ and 17 ♀♀ found dead in trap and 74 flies found dead in liquid.

Experiment 2. *Common food-stuffs.*

Date:—August 31st–September 1st.
General weather conditions:—Bright, hot.
Duration of experiment:—Experiment substances, 48 hours.
Control substances, 24 hours.

Exp.	Substance	Amount	Flies caught ♂	♀	Total	Control substance	Amount	Flies caught ♂	♀	Total
1	Vanilla extract (ordinary)	20 c.c.	17	27	44*	Grape juice	10 c.c.	49	55	104
2	Lemon extract	25 c.c.	2	10	12	,, ,,	10 c.c.	3	4	7
3	Spirit of vinegar	25 c.c.	3	5	8	,, ,,	10 c.c.	22	51	73

* Including 2 found dead in trap and 3 flies dead in liquid. Five flies found dead in grape juice. Control substances were only used during the second 24 hours of this experiment.

In these experiments the "Amount" given denotes the total quantity of the substance used for the three interpositions: at the end of each interval of time the substances were renewed.

The figures show that banana is the most attractive substance, grape juice, vanilla extract, lemon extract, brown sugar and water, spirit of vinegar and glacial acetic acid following in order.

The strong grape juice controls in Exp. 2 attracted the flies away from the vanilla extract and lemon extract: this is shown by the fact that, during the first 24 hours, while no controls were used, the figures for the experiment substances were vanilla extract 25, lemon extract 12, spirit of vinegar 3.

It may be well here to give the results of these two experiments in percentages, to give an idea of the proportion of flies out of 100 which would enter each trap.

Experiment 1		*Experiment* 2	
Banana	74	Grape juice	66
Vanilla extract	21	Vanilla extract	24
Brown sugar and water	4	Lemon extract	6
Acetic acid (glacial)	1	Spirit of vinegar	4
	100		100

The figures for the controls are, of course, derived by calculation, allowance being made for the three traps instead of one in each case, and for the duration of time in the second case. In both cases the position of vanilla extract appears to be approximately the same, showing that the figures are reliable.

It may be added that the number of flies caught in the weak controls in Exp. 1 are in a rough direct proportion to their experiment substances, so that it would appear that they had, themselves, a definite attraction to the flies brought into their proximity by the strongly attractive agents, and doubtless had the effect of compensating for the error due to flies leaving an experiment substance and flying to another.

Experiment 3. *The increase in attraction of banana due to fermentation and decomposition.*

Date:—August 28th–September 2nd.
General weather conditions:—Du'l and cool during first period.
Hot and bright after.
Total duration of experiment:—138 hours.

Period	Duration	Flies alive in trap			Flies dead in trap			Total flies caught		
		♂	♀	Total	♂	♀	Total	♂	♀	Total
1	23 hours	33	75	108	0	1	1	33	76	109
2	43 ,,	191	192	383	147	203	350	338	395	733
3	24 ,,	—	—	—	—	—	—	49	68	117
4	24 ,,	4	28	32	12	21	33	16	49	65
5	24 ,,	0	0	0	0	0	0	0	0	0

By an unfortunate oversight, the numbers of flies found dead, and of those found alive in the trap were not differentiated during Period 3.

The positively chemotropic stimulus in banana and in grape juice is due to products of fermentation. To prove this beyond doubt a fresh banana was pealed and cut into two halves. One half was crushed into a glass dish and set under a trap.

However, it is clearly seen that, during decomposition, banana becomes increasingly attractive, and the attractive power passes off as the putrescent mass dries off. The banana used was rather overripe at the start, and the results of Exp. 5 in Section II prove that the attractive qualities are exceedingly small when the fruit is rather unripe, an increase in the numbers being again shown when decomposition has set in, in Exp. 6.

It will have been observed that, not only with banana, but also with vanilla extract as baits, there is a high percentage of mortality amongst both male and female flies after they have entered the traps, and an increasing mortality as decomposition proceeds in banana.

This cannot be attributed to the fact that the flies were at the extreme limits of their life-existence, for a very large proportion of the female flies contained eggs, and it is clear to a degree that, in the case of banana, the decomposition and fermentation products have a deleterious effect just as strong oil of citronella has upon Dacus (Howlett)[1].

It does not imply, however, that the decomposition products are a stimulus to oviposition, for the flies were directly attracted away from manure, where they were breeding, though it must be admitted that some reagents in banana and manure may be similar in composition as an enticement to breeding. The mortality in vanilla extract is evidently attributable to alcoholic evaporation. The large proportion in many cases of female to male flies is merely due to the fact that the former were most abundant in the locality.

With regard to the attractive features of glacial acetic acid and spirit of vinegar, these substances might be found to have increased stimulating powers when diluted to an optimum solution (see Barrows)[2]. The latter reagents also produce mortality to a slight degree, grape juice, when fermenting to a considerable degree, and reference is here made to experiments with alcohols, aldehydes and acids described in Section II, proving that this is due to the products of alcoholic, aldehydic and acidic fermentation of organic substances.

Banana, as being the most attractive substance to the house-fly, is used as the basis of investigation in the next section.

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[1] *Trans. Ent. Soc. Lond.* Part II, pp. 412–418.

[2] *Journ. Exp. Zoology,* Baltimore, Md. pp. 515–537.

SECTION II.

EXPERIMENTS WITH THE DECOMPOSITION PRODUCTS OF BANANA AND SUBSTANCES ALLIED TO THEM.

It is possible to deduce the approximate composition of banana from E. Munroe Bailey's "Studies on the Banana," *Journal of Biological Chemistry*, I. 1, p. 355.

Ripe Banana.

	% %	
Solids	21·5–34·5	Water difference from 100.
Protein	0·6– 2·1	
Invert sugar	3·1–21·4	When invert high, cane low and *vice versa.*
Cane sugar	0·2–17·5	
Total sugar	12·3–25·6	
Other nitrogen free extract	2·0–10·7	
Fibre	0·2– 1·2	
Ash	0·7– 1·1	

Unripe Banana.

Unripe banana contains insoluble carbohydrates, which, in the presence of air, give place to soluble carbohydrates when the fruit ripens.

Thus the proportion of soluble and insoluble carbohydrates as *dextrose* is

	Soluble	Insoluble	Total
In unripe banana	1·3	25·2	26·5
In ripe banana	17·1	1·9	19·0

The decomposition products therefore contain few nitrogen compounds, and ferment to the decomposition products of carbohydrates, such as alcohols, acids and their compounds.

The method of experiment adopted was similar to that in Section I, but the traps were placed in a glass house on a table 4 feet from the ground and in a straight line. Instead of employing control substances, each pair of traps was baited with a known quantity of the same substance.

The distance between each pair of traps was about 4 feet, those containing similar substances being placed 6 inches apart. The pairs were interposed as in the previous experiments.

The first series was carried out to determine the general qualities of carbohydrates in an unfermenting condition. For the purpose, brown sugar, white sugar, and starch were used in a dry condition; water was intentionally not added to them, as moist substances always show a certain attraction, when not actually repellant, on account of the water contained by them.

Experiment 4. *Carbohydrates.*

Date:—September 10th–12th.
General weather conditions:—Cool, rain.
Duration of experiment:—69 hours.

Substance	Amount	Flies caught			Percentage
	oz.	♂	♀	Total	
Brown sugar	4	4	6	10	84
White sugar	4	0	0	0	0
Starch	4	1	1	2	16
					100

In spite of the small numbers caught, there was an abundance of flies round the traps, and the results show that carbohydrates in this condition are very moderately attractive.

The odour of banana is strongly reminiscent of amyl acetate, and minute quantities of the latter substance suggest that amyl compounds might well be derived from ripening and decomposition products through fermentation.

Experiments were accordingly carried out to test the attractiveness of these substances, relating to each other and to decomposing banana.

They bear the formulae: amyl alcohol, $CH_3(CH_2)_4OH$; amyl acetate, $CH_3(CH_2)_4CH_2COOH$; valerianic aldehyde, $CH_3(CH_2)_3CHO$; valerianic acid, $CH_3(CH_2)_3COOH$.

Though closely allied, the odours which they give off are very different, the acid being especially pungent.

Valerianic aldehyde took some time to prepare in the laboratory, and was therefore not available for experiment until later.

In the first of the two following experiments, an unripe pealed banana was used: this was afterwards crushed and allowed to ferment in a covered glass vessel for four days, at the end of which time it was used for the second experiment. The liquids were used in a pure, undiluted state in all subsequent experiments.

This at once points to the fact that, whilst unripe and not decomposed banana is very much less attractive than amyl alcohol and amyl acetate, on decomposition it becomes more attractive than amyl acetate and valerianic acid. The figures in Exp. 6 give no idea of the relative strengths of amyl acetate and valerianic acid, as the former substance held the most favourable position, the short duration of the experiment, for obvious reasons, preventing interposition of the traps.

Experiment 5. *Decomposition products of banana.*

Date:—September 30th–October 1st.
General weather conditions:—Bright, warm.
Duration of experiment:—44 hours.

Substance	Amount c.c.	Flies caught			Percentage
		♂	♀	Total	
Amyl alcohol	60*	5	4	9	41
Amyl acetate	60*	4	8	12	54
Banana (unripe)	—	1	0	1	5
					100

* Denotes 20 c.c. for each period.

Five flies were found dead in the amyl acetate trap.

Experiment 6. *Decomposition products of banana.*

Date:—October 5th–6th.
General weather conditions:—Warm, dull.
Duration of experiment:—24 hours.

Substance	Amount c.c.	Flies caught			Percentage
		♂	♀	Total	
Amyl acetate	20	14	18	32	39
Valerianic acid	20	11	5	16	19
Banana (decomposed 4 days)		18	17	35	42
					100

Two flies were found dead in the valerianic acid trap.

Experiment 7.

Date:—October 2nd–3rd.
General weather conditions:—Bright, warm. At termination, cool with some rain.
Duration of experiment:—69 hours.

Substance	Amount c.c.	Flies caught			Percentage
		♂	♀	Total	
Amyl alcohol	28	1	6	7	7
Amyl acetate	28	5	15	20	19
Valerianic acid	28	27	51	78	74
					100

Three flies found dead in amyl acetate, 6 in amyl alcohol, and 12 in valerianic acid traps.

Here are shown the relative attractive powers of these three liquids, and it is seen that they fall into the order in which one would expect them to be formed during fermentation, with increased positive chemotropic effects.

After October 5th the flies unfortunately became lethargic, and the following figures suffer very much from the insects being in this condition.

It is therefore not possible to determine the exact position of valerianic aldehyde in relation to the above reagents. Exp. 9 shows it to be strongly attractive under the prevailing conditions, but does not give an idea as to its holding a place between amyl acetate and valerianic acid, which, on the face of what has gone before, is quite probable.

To come to some conclusion as to what arrangement of molecular grouping furnishes these substances with their positive chemotropic powers, records were taken of the numbers of flies caught respectively by four alcohols, three aldehydes, and three acids—as here named with their chemical formulae:

Methyl alcohol, $H.CH_2OH$; ethyl alcohol, CH_3CH_2OH; amyl alcohol, $CH_3(CH_2)_3CH_2OH$; benzyl alcohol, $C_6H_5.CH_2OH$.

Valerianic aldehyde, $CH_3(CH_2)_3CHO$; benzaldehyde, C_6H_5CHO; cinnamaldehyde, $C_6H_5(CH)_2CHO$.

Valerianic acid $CH_3(-CH_2)_3COOH$; benzoic acid + ethyl alcohol, $C_6H_5.COOH + CH_3CH_2OH$; cinnamic acid + ethyl alcohol, $C_6H_5(CH)_2COOH + CH_3CH_2OH$.

All these were used undiluted, except for the two solids benzoic acid and cinnamic acid, of which saturated solutions were prepared in pure ethyl alcohol.

Experiment 8. *Alcohols.*

Date:—October 6th–7th.
General weather conditions:—Warm, dull.
Duration of experiment:—23 hours.

Substance	Amount c.c.	Flies caught		
		♂	♀	Total
Methy alcohol	20	0	0	0
Ethyl alcohol	20	1	2	3
Amyl alcohol	20	0	1	1
Benzyl alcohol	20	0	1	1

Percentages are not given, as the number of the flies caught is insufficient. The only fly caught by benzyl alcohol probably entered the trap by accident.

Ethyl and amyl alcohols are the only two attractive ones.

Experiment 9.

Date:—October 7th–9th.
General weather conditions:—Warm, dull.
Duration of experiment:—45 hours.

Substance	Amount c.c.	Flies caught ♂	♀	Total
Valerianic aldehyde	20	3	6	9
Benzaldehyde	40	0	3	3
Cinnamaldehyde	40	1	0	1

Experiments with oil of bitter almonds point to the fact that benzaldehyde is not positively chemotropic, and the same applies to cinnamaldehyde.

Experiment 10. *Acids.*

Date:—October 6th–9th.
General weather conditions:—Warm, dull.
Duration of experiment:—69 hours.

Substance	Amount c.c.	Flies caught ♂	♀	Total	Percentage
Valerianic acid	20	17	28	45	71
Benzoic acid in 100 % ethyl alcohol	45	9	7	16	26
Cinnamic acid in 100 % ethyl alcohol	70	1	1	2	3
					100

The last figures are more satisfactory, and give valerianic acid a percentage close to that of Exp. 7 when this liquid was used in company with an alcohol and an acetate. From observations made upon solid benzoic and cinnamic acids it is probable that these substances owed their attractive features solely to the ethyl alcohol in which they were dissolved, and benzoic acid may actually be negatively chemotropic.

A curious observation was made upon flies exposed to cinnamic acid, in that they show a prolonged immunity to the fumes of hydrocyanic acid gas. The effect of cinnamic acid is therefore probably antidotal to the insects.

The conclusions to be drawn are as follows:

1. Saturated alcohols, aldehydes and acids are positively chemotropic in products of fermentation, as far as amyl compounds are concerned.

2. Alcohols, aldehydes and acids containing the methyl group CH_3 are positively chemotropic, except in cases where their molecular weight is about 30 (methyl alcohol) or below, the chemotropic stimulus being

aggravated where the methyl group is augmented by union with $(CH_2)_x$.

3. Compounds containing the benzene ring are unattractive though not necessarily negative. These are unsaturated.

4. Amyl compounds are probably increasingly attractive in the order in which they are formed during fermentation and decomposition.

5. If, in this series, valerianic aldehyde is less attractive than amyl acetate or amyl alcohol, then it is probable that the aldehyde group, in all compounds containing it, is to a certain extent negatively chemotropic.

There is evidently no relation between volatility and chemotropic action.

Note was made of the rates of evaporation during the experiments, and these are given below, the substances being arranged in order of assumed attractive power.

	Substance	Original amount c.c.	Final amount c.c.	Loss in volume c.c.	Time hours
1	Valerianic acid	20	19	1	23
2	Valerianic aldehyde	20	7·5	12·5	23
3	Amyl acetate	20	14	6	24
4	Amyl alcohol	20	16	4	23
5	Ethyl alcohol	20	0 (water)	20	23
6	Cinnamic acid in ethyl alcohol	20	Crystalline	—	23
7	Benzyl alcohol	20	19	1	23
8	Benzaldehyde	20	Crystalline	—	22
9	Methyl alcohol	20	0 (water)	20	23
10	Cinnamaldehyde	20	20	0	23
11	Benzoic acid in ethyl alcohol	20	Crystalline	—	23

It is sufficient at this stage to point out that saturated compounds contained in fermenting vegetable substances and containing the molecular group $CH_3(CH_2)_x$ may constitute the source by which the house-fly is guided to its food.

SECTION III.

ESSENTIAL OILS.

The experiments in this section were carried out under the same conditions as those in the last.

To give an idea of the number of house-flies caught by the traps in their respective positions, a control record was taken with a known quantity of grape juice. The results were as follows:

Experiment 11. *Control with grape juice.*

Date:—September 8th–10th.
General weather conditions:—Cool, some rain.
Duration of experiment:—48 hours.

Trap	Substance	Amount c.c.	Flies caught ♂	Flies caught ♀	Flies caught Total
A	Grape juice	20	14	17	31
A′	,, ,,	20	32	28	60
B	,, ,,	20	44	23	67
B′	,, ,,	20	6	13	19
C	,, ,,	20	9	2	11
C′	,, ,,	20	12	12	24

The average for each pair of traps (A, A′; B, B′; C, C′) is, then, about 70 flies for the 48 hours. Traps B and A′ are seen to be in the most favourable positions, and the pairs A, A′ and B, B′ are credited with the highest number. By interposition the differences are eliminated in the following experiments.

It might be thought that many of the sweet-smelling essential oils are attractive to the house-fly, but this is here shown to be a misconception, for many of them are, to a certain degree, actually repellent.

Experiment 12.

Date:—September 15th–18th.
General weather conditions:—Warm, bright.
Duration of experiment:—76 hours.

Substance	Amount c.c.	Flies caught ♂	Flies caught ♀	Flies caught Total
Cedar oil	20	0	0	0
Oil of juniper berries	20	0	1	1
Oil of *Pinus Sylvestris*	20	0	0	0

At the same time, three traps were placed in the stable used for the experiments in Section I for 26 hours. The figures were exactly similar to the above, and in both cases the female fly in the juniper oil trap was dead. It is probable that the two flies entered by accident.

Experiment 13.

Date:—September 18th–21st.
General weather conditions:—Warm, bright.
Duration of experiment:—46 hours.

Substance	Amount c.c.	Flies caught ♂	Flies caught ♀	Flies caught Total
Orange oil	20	0	1	1
Lemon oil	20	0	0	0
Citronella oil	20	0	1	1
Camphor oil	20	0	0	0
Clove oil	20	0	0	0
Eucalyptus oil	20	0	0	0

Here again the oils are seen to be almost totally unattractive. The stray insects which enter the traps do so merely by accident.

Eucalyptus oil is said to contain valerianic acid, and it is noteworthy that no flies were attracted to it.

It has been demonstrated that these essential oils are unattractive but it still remains to be shown if any of them are actually repellent, i.e. negatively chemotropic.

For this purpose, the traps were used in the same positions as before, but under each were placed two dishes—one containing a known quantity of an essential oil, and the other a known quantity of grape juice.

At the end of each period of time the traps were changed as to their positions, a new supply of grape juice being used for each period, and the oils being left to evaporate through the whole time.

This was done particularly to avoid fermentation of the grape juice, and total evaporation, for the amount of alcohol formed in the fermenting liquid volatilises at a high speed, leaving behind carbohydrates in the form of sugar.

Experiment 14. *Repulsion by essential oils.*

Date:—September 21st–24th.
General weather conditions:—Very hot, storms at termination.
Total duration of experiment:—72 hours.

	Substance	Amount at start c.c.	Amount at finish	Flies caught								
				Period 1, 24 hours			Period 2, 24 hours			Period 3, 24 hours		
				♂	♀	Total	♂	♀	Total	♂	♀	Total
1	Lemon oil	14	0·75 c.c.	0	1	1	0	0	0	251	240	491
	Grape juice	30	renewed at each period									
2	Orange oil	14	1·0 c.c.	0	0	0	12	9	21	43	52	95
	Grape juice	30	renewed at each period									
3	Citronella oil	14	4·0 c.c.	1	1	2	0	0	0	45	69	114
	Grape juice	30	renewed at each period									

It would appear that, although strongly repellent at first, these oils lose their repellent properties with evaporation, and further that the attractive qualities of grape juice emanate through the oils, thus approximating insects to the traps, into which they rush in great numbers when the repellent properties disappear.

An experiment made shortly after, substituting camphor oil for citronella oil, and cedar oil for lemon oil, bears this out. Flies were still abundant round the traps.

Experiment 15. *Repulsion by essential oils.*

Date:—September 26th–28th.
General weather conditions:—Cool, bright.
Duration of experiment:—42 hours.

	Substance	Amount at start c.c.	Amount at finish c.c.	Flies caught		
				♂	♀	Total
1	Orange oil	14	6·5	14	6	20
	Grape juice	30	—			
2	Camphor oil	14	3·0	0	1	1
	Grape juice	30	—			
3	Cedar oil	14	11·0	13	9	22
	Grape juice	30	—			

It must be remembered that these figures are comparable to the first two periods of Exp. 14, and orange oil holds the same place in both cases.

The latter oil appears to lose its repellent power sooner than lemon oil and citronella oil.

Experiment 16. *Repulsion by essential oils.*

Date:—September 25th–26th.
General weather conditions:—Cool, bright.
Duration of experiment:—27 hours.

	Substance	Amount at start c.c.	Amount at finish	Flies caught		
				♂	♀	Total
1	Camphor oil	14	6·0 c.c.	34	22	56
	Grape juice	30	—			
2	Eucalyptus oil	14	6·0 c.c.	32	29	61
	Grape juice	30	—			
3	Oil of bitter almonds	14	Crystalline	99	90	189
	Grape juice	30	—			

None of these can be truly repellent except camphor oil, and traps set alone with oil of bitter almonds, a substance with a smell resembling benzaldehyde, show that the latter is certainly not attractive. The same has also been demonstrated with cedar oil and eucalyptus oil. The high figures for camphor oil were no doubt due to the enormous numbers of flies round the traps, and another experiment was made to certify this.

Experiment 17. *Repulsion by essential oils.*

Date:—September 28th–30th.
General weather conditions:—Bright, cool.
Total duration of experiment:—45 hours.

	Substance	Amount at start c.c.	Amount at finish	Flies caught					
				Period 1, 22 hours			Period 2, 23 hours		
				♂	♀	Total	♂	♀	Total
1	Camphor oil	14	·1 c.c.	0	1	1	1	0	1
	Grape juice	20	renewed at each period						
2	Cedar oil	14	13 c.c.	1	4	5	7	1	8
	Grape juice	20	renewed at each period						
3	Oil of *Pinus Sylvestris*	14	3·5 c.c.	1	0	1	0	0	0
	Grape juice	20	renewed at each period						

The author wishes to make it clear that he does not consider the experiments upon actual repulsion by essential oils in any way final until further observations are made in a similar direction. This applies to eucalyptus and camphor oils, two substances of almost indistinguishable odour when in the pure state, in special.

Weather conditions may have much to do in determining the repellent qualities when placed in juxtaposition with attractive substances, and when flies are in great numbers, it is not impossible that they should invade, to them malodorous compounds, to reach positively chemotropic reagents.

The conclusions drawn, then, are subject to revision.

1. Essential oils are unattractive to the house-fly in general.

2. Certain essential oils evoke negatively chemotropic stimuli, these being oil of *Pinus Sylvestris*, orange oil, lemon oil, citronella oil, oil of juniper berries, and possibly camphor oil.

3. Certain essential oils are inactive in raising stimuli, these being cedar oil, eucalyptus oil, and oil of bitter almonds. They may themselves be neither positively, nor negatively, chemotropic in action, but probably have slight negative features.

4. During evaporation, the repellent actions pass off, soonest in orange oil and later in lemon oil, citronella oil, and oil of *Pinus Sylvestris*, and some coordination may occur in relation to the rate of evaporation and the retention of repellent qualities.

NOTE:—Essential oils are not repellent to all insects. Gryllidae were repeatedly found in camphor, lemon, citronella oils; also some Diptera of the Genus *Culex* (though oil of citronella is strongly repulsive to these), and Lepidoptera of the families *Noctuidae* and *Geometridae.*

A single *Stomoxys calcitrans* Linn. was found in oil of juniper berries, and one *Calliphora irridescens* Des.

Citronella oil has already been mentioned as attracting two species of Dacus, and oil of bitter almonds attracts species of Thrips (Howlett)[1].

On September 23rd, the traps baited with orange oil and grape juice contained 3 dead male flies and 1 dead female out of a total of 12 males and 9 females.

On September 24th 4 flies were floating in lemon oil used in conjunction with grape juice out of a total of 251 males and 240 females.

In both instances these may have fallen into the oil dishes by accident after feeding heavily on the grape juice.

SECTION IV.

RECORD OF OTHER INSECTS OBSERVED DURING THE EXPERIMENTS.

The following table gives a record of Diptera attracted to substances used in the various experiments of Sections II and III, but it must be remembered that the traps employed were not suitable for the collection of many of the smaller species, of which a considerable number must have escaped.

The various re-agents are designated by letters, as below:

A, Amyl alcohol; B, Amyl acetate; C, Valerianic aldehyde; D, Valerianic acid; E, Cinnamic aldehyde; F, Cinnamic acid in ethyl alcohol; G, Oil of bitter almonds; H, Oil of juniper berries; I, Grape juice; J, Banana; K, Brown sugar. The numerals represent the number of insects attracted to that particular bait.

Muscina stabulans Fall. E 1, F 3, I 10, J 3: total 17. *Sarcophaga assidua* Walk. D 3, I 15, J 1: total 19. *Sarcophaga helicis* Town. B 1, I 1: total 2. *Fannia canicularis* Linn. A 3, D 1, F 1, G 1, I 3, J 7: total 16. *Drosophila ampelophila* Loew. A 1, B 2, I 2: total 5. *Stomoxys calcitrans* Linn. A 2, H 1: total 3. *Calliphora irridescens* Des. G 1. *Calliphora erythrocephala* Meig. I 2. *Lucilia caesar* Linn. I 2. *Lucilia sericata* Meig. I 1. *Phormia regina* Meig. I 1. *Phorbia fusciceps* Leff. D 1. *Limosina* sp. B 2. *Borboridae* A 4, D 2: total 6. *Spilogaster* sp. K 1. *Chironomus* sp. B 1. *Boetechenia latisterna* Pack. I 1. *Cynomia cadaverina* Des. J 1.

It is noticeable that only one fly, *Fannia canicularis* Linn., was attracted to a substance containing the benzene ring as well as to substances containing the $CH_3.CH_2$ group, and, in the case of the former, only one fly was found in each trap. On the other hand, *Muscina stabulans* Fall. occurred only in substances containing the benzene ring.

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[1] *Journal of Economic Biology*, Vol. IX, No. 1, pp. 21–23.

Sarcophaga assidua Walk. was a common insect at the time, and was attracted to valerianic acid, grape juice, and banana only. Howlett has observed that other species of *Sarcophaga* are strongly influenced by a solution of Skatol, which contains the benzene ring and a methyl group. This substance is found in faeces. Its effect upon *Sarcophaga* seems to be to guide the female to places for oviposition. It may be that the benzene ring reacts positively to fertile females, and products of fermentation to individuals generally as a guide to food only.

Amongst the other insects caught in these experiments, the Coleoptera, *Epitrix parvula* Fab., and *Chaetocnema denticulata* Illiger, occurred in valerianic aldehyde and amyl acetate respectively—one specimen of each.

Gryllidae were often found in traps baited with essential oils, namely, citronella, lemon, and camphor oil: also in traps baited with amyl alcohol and methyl alcohol, but in the latter cases seldom more than one in each trap.

Thysaneura of the Genus *Lepidocyrtus*, and, on Mr Banks' authority, closely allied to, but distinct from *L. metallicus*, were attracted in some numbers to amyl acetate, valerianic acid, and amyl alcohol. These insects were not influenced by benzaldehyde or cinnamic acid.

Finally, it is not considered that the *Valerianic* series of substances is necessarily the series acting most positively to the house-fly, and it is suggested that experiments be carried out with the *Butyric* series.

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OBSERVATIONS ON THE INSECT FAUNA OF PERMANENT PASTURE IN CHESHIRE

BY HUBERT M. MORRIS, M.Sc.

(*Entomological Dept., Institute of Plant Pathology, Rothamsted Experimental Station, Harpenden.*)

(With 1 Text-fig.)

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1. INTRODUCTION.

THIS investigation was carried out between September 1916 and September 1917, with the object of obtaining as much information as possible with regard to the insect fauna of a permanent pasture. The field in which the investigation was carried out was chosen as being as nearly as possible typical of all such fields in the surrounding district, which comprises the central and eastern parts of Cheshire.

I am indebted to Dr A. D. Imms for assistance in many ways throughout this investigation; to Mr T. J. Young, M.Sc., formerly Principal of the College of Agriculture, Holmes Chapel, Cheshire, for permission to use the field in which it was carried out; and to the following gentlemen for assistance in the identification of many of the insects taken: Mr J. M. Brown, B.Sc.; Mr H. Bury, B.A.; Mr J. Collin; Mr G. T. Lyle; the Rev. F. D. Morice, M.A.; Mr C. Morley; the Rev. J. Waterston, B.D., B.Sc.

The investigation was carried out from the Department of Agricultural Entomology, Manchester University, and the work finally completed at Rothamsted.

2. DESCRIPTION OF THE DISTRICT.

This region is mainly devoted to the production of milk, and a large proportion of the area is occupied by permanent pastures for the grazing of the dairy cattle. The fields in this district are usually small compared with those in other parts of England, about ten acres being a common area.

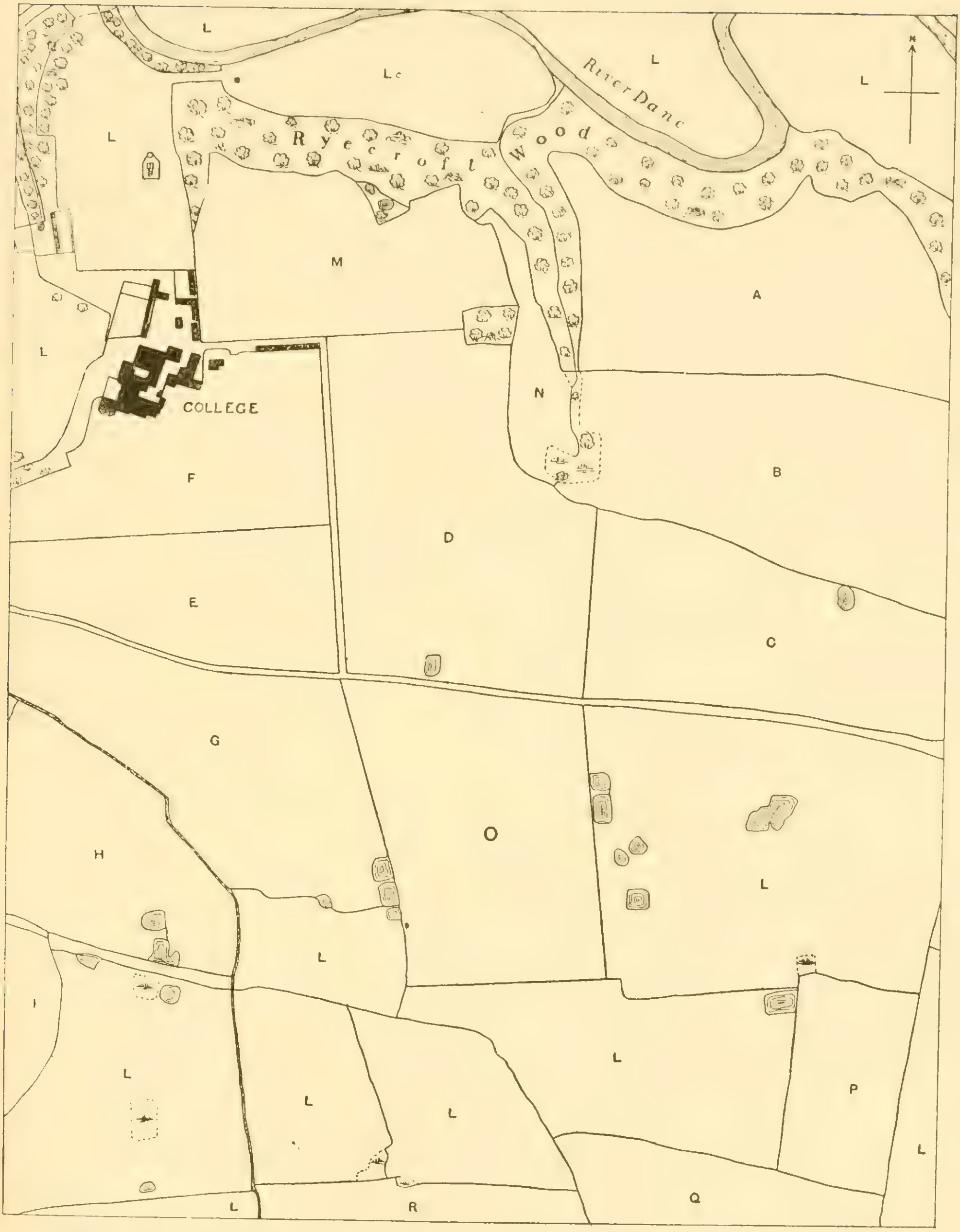
They are almost universally separated by hedges of hawthorn, often very much overgrown, and overrun with bramble and dog-rose, together with holly and occasionally furze-bushes. These hedges often stand on a low bank and, in addition to the above mentioned shrubs, usually contain a few trees, the commonest being the oak. Similar trees are also often found away from the hedges, scattered about the fields. These hedges and trees give the district, when seen from a distance or from a slight elevation, a very well-wooded appearance, which, however, is not so noticeable on a closer examination. These trees are almost always rather small and stunted owing, probably, to their being scattered about singly and not usually gathered together in woods or coppices.

Another very noticeable feature of the district is the number of ponds which are present, several often being found in a single field. Many of these ponds have formed where pits were dug in order to obtain the marl which underlies this district, and which was formerly spread over the fields, owing to the general shortage of lime in the soil of the district.

The small wood indicated on the map consists of beech, oak, alder, ash, and sycamore, with some holly, hawthorn, mountain ash, and elm, with an undergrowth of elder and hazel.

The crops grown on the arable fields in the immediate neighbourhood during the period of the investigation were:

Field	1916	1917
A	Potatoes; oats	Oats; wheat
B	Wheat; oats	Oats; clover and grass mixture
C	Potatoes; mangolds; swedes	Wheat; oats
D	Wheat; oats; rye grass	Oats; clover and grass mixture
E	Clover and grass mixture	Clover and grass mixture
G	Clover and grass mixture; oats	Mangolds; swedes; oats; potatoes
H	Oats	Clover and grass mixture
I	Clover and grass mixture	Oats
M	Temporary pasture laid down 1914	
N	Nursery of seedling conifers sown 1916, previously pasture	
P	Potatoes	Oats
Q	Oats	Oats
R	Wheat; oats	Swedes; mangolds; clover and grass mixture


L
Lc
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River Dane
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Ryecroft Wood
M
A
L
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COLLEGE
B
F
D
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Q

Fig. 1. Map of the locality in which the field under observation was situated. Reduced from Ordnance Survey map to a scale of 10·75 inches = 1 mile.

The area marked F on the map is the College garden, in which many kinds of fruit and vegetables are grown. The enclosures marked L are permanent pastures. The enclosure marked O is the field in which the investigation was carried out.

3. DESCRIPTION OF THE FIELD.

The field in which this investigation was carried out forms part of the farm of the Holmes Chapel College of Agriculture, and is known as the "Lane Field." It lies at an altitude of about 220 feet above sea level, and has an area of about 10·2 acres.

The Lane Field is roughly rectangular in shape, the longer sides running almost due north and south, with the shorter sides approximately at right angles to them. The field is surrounded on all four sides by hawthorn hedges, those on the north, east and west sides being well grown, thick, and kept fairly clean. The hedge on the south side is older and thinner, the bushes not having been cut back, and it is more overrun with brambles than the other hedges, and also contains a few furze bushes. In these hedges grow several trees, chiefly oaks, with one or two ashes, sycamores, and alders, and there are also six oak trees in a line east and west across the centre of the field, which, with a slight depression beside which they stand, appear to mark the position of a former hedge, which has been removed many years.

On the west side, near the south-west angle, is a row of three small ponds lying along the boundary of the field, and on the east side a row of five similar ponds lies just on and beyond the boundary of the field, while just outside the south-east corner is a small area which is usually rather swampy, where a similar pond has been filled in.

The field is almost level, there being a slight slope from the east side down to the west, but this does not amount to more than about five feet. The lowest part is the north-western portion which is liable to become water-logged in very wet weather, and may then have water standing in small pools on it for a short time.

The soil of the College Farm "consists almost entirely of a strong loam of Glacial Drift overlying the Triassic rocks. It shows variations in places from a pure Boulder Clay to a lighter class of sandy loam, the latter occurring in small patches here and there, and being more marked round the College buildings and near the main road. There is an outcrop of the underlying Keuper marl along the broken hillside bordering the River Dane, and an area of alluvial deposit immediately adjacent to the stream" (College Prospectus).

The character of the soil of the field varies somewhat, that of the north-western portion probably containing a larger proportion of clay, while that of the south-eastern portion is more sandy.

The Lane Field has been a pasture for at least thirty or forty years, and possibly longer, no one in the neighbourhood appearing to remember it having been ploughed. For several years prior to 1914 the field had received a yearly dressing of bone-meal, but from that date to the period during which the observations were carried out it had been unmanured. The field is regularly grazed by sheep, cattle and horses.

4. CHEMICAL FEATURES OF THE AREA.

It was considered advisable, in order to define the conditions in the selected field as exactly as possible, to carry out both chemical and mechanical analyses of the soil of the field.

Chemical Analysis (in percentages).

Iron (Fe_2O_3)	2·152	Phosphorus (P_2O_5)	0·348
Calcium (CaO)	0·57	Aluminium (Al_2O_3)	2·360
Magnesium (MgO)	0·609	Potassium (K_2O)	0·60
Nitrogen (N)	0·210	Sulphates (SO_3)	0·066

Mechanical Analysis.

Moisture	1·86	Fine sand (0·2 to 0·04 mm.)	28·53
Organic matter	6·21	Silt (0·04 to 0·01 mm.) ...	16·94
Stones (over 3 mm.) ...	0·70	Fine silt (0·01 to 0·002 mm.)	6·71
Fine gravel (3·0 to 1·0 mm.)	1·29	Clay (below 0·002 mm.) ...	4·46
Coarse sand (1·0 to 0·2 mm.)	32·40		

For the above analyses samples of soil were taken from various parts of the field, to a depth of nine inches, these samples being afterwards mixed. At a depth of about a foot a stiff stratum was encountered, which appeared to have a much higher proportion of clay. Below a depth of about six inches there was very little organic matter, which is accounted for largely by the fact that most of the grasses were of the shallow rooted kinds.

5. BOTANICAL FEATURES OF THE AREA.

Relatively few species of plants occurred in the field. The predominant grasses were the Crested Dogs-tail (*Cynosurus cristatus*) and the Bent grasses (*Agrostis* spp.). There were, however, patches where Cocksfoot (*Dactylis glomerata*) and Sweet Vernal grass (*Anthoxanthum odoratum*) predominated. An analysis of a typical area gave the following results in percentages by weight:

Gramineae		
Agrostis alba and *A. vulgaris*	44·1	
Cynosurus cristatus	30·3	
Lolium perenne	9·4	
Poa spp.	3·5	87·3
Leguminosae		
Trifolium spp.		5·6
Other orders (regarded as weeds)		7·0

Under the latter category the following may be mentioned:

Abundant: *Ranunculus acris, R. repens, Bellis perennis, Brachythecum rutabulum.*

Common: *Holcus lanatus, Plantago lanceolata, Urtica dioica, Carduus arvensis, Cerastium triviale.*

Occasional: *Polygonum persecaria, Plantago major, Ajuga reptans, Hieracium* spp., *Luzula campestris, Rumex acetosa.*

Urtica dioica occurred in two or three patches in the field and also in the hedges in a few places. *Luzula campestris* occurred in the lower and damper part of the field.

The hedge-bottoms were fairly clean owing to those of the College farm being occasionally dug over. In addition to most of the above species, the hedges also contained species of *Rumex*. A moss, probably *Brachythecum rutabulum*, formed an almost continuous covering to the soil, although obscured by the taller plants from casual observation.

6. METHODS OF INVESTIGATION.

The investigation was carried out in the following manner. The turf and soil of an area ten inches square was removed entire to a depth of two inches. The soil below was then removed in layers, each layer being examined separately so that the depth at which the insects occurred could be determined. This examination was carried out in the field, and on several occasions the soil was examined to a depth of two feet,but as very few insects were found at a greater depth than two inches, one foot was usually considered a sufficient depth to examine.

The upper layer, consisting of the turf and surface soil, was placed in a box and taken to the laboratory, as, owing to the presence of roots and of almost all the soil insects, this sample required more careful examination.

Of the larvae and pupae obtained, some were killed and preserved immediately, while an attempt was made to rear the adult insects from the others, on account of the difficulty of identifying larvae. In some cases this was successfully accomplished, but in a number of cases it did not succeed.

In addition to the examination of the insects actually present in the soil, large numbers of adult insects were obtained by sweeping the herbage with a net, a large proportion of which were insects with soil inhabiting larvae, but in addition to these, other species were taken whose presence was due to accident or to their having migrated from their breeding place.

7. Insects occurring in the Soil of the Area.

(The figures in brackets indicate the months during which the species occurred; where there are two numbers, the upper indicates the month and the lower the number of individuals found.)

Collembola.

Entomobryidae. *Isotoma viridis* Bourl. Schott (1, 2, 7, 8, 12); *I. olivacea* Tullb. var. *grisescens* (Schaff.) (1, 12); *Isotomurus palustris* (Mull.) (1, 2, 7, 8, 11, 12); *Entomobrya multifasciata* (2, 7); *Lepidocyrtus cyaneus* (12).

Achorutidae. *Onychiurus armatus* (Tullb.) (1); *Achorutes armatus* (Nic.) Tullb. (11); *A. manubrialis* Tullb. (1, 11).

Sminthuridae. *Sminthurus viridis* (Linn.) Lubb. (1, 6, 7, 8, 10); *Sminthurinus aureus* (Lubb.) var. *ochropus* (Reut.) (11); *S. aureus* var. 4-*lineatus* (7).

Rhynchota.

Aphidae spp. ($\frac{7}{1}$, $\frac{11}{2}$, $\frac{12}{1}$); spp. ($\frac{1}{1}$, $\frac{3}{2}$).

Thysanoptera.

Spp. ($\frac{7}{6}$, 8, $\frac{11}{2}$, $\frac{12}{12}$).

Lepidoptera.

Larvae and pupae.

Triphaena pronuba L. ($\frac{1}{1}$, $\frac{6}{1}$); spp. ($\frac{9}{1}$, $\frac{11}{1}$, $\frac{12}{3}$).

Coleoptera.

Adults.

Carabidae. *Amara apricaria* Pk. ($\frac{3}{2}$); *Bembidium obtusum* Sturm. ($\frac{7}{1}$); *Clivina fossor* L. ($\frac{8}{1}$, $\frac{11}{1}$); *Anchomenus sexpunctatus* L. ($\frac{12}{1}$); *Calathus melanocephalus* L. ($\frac{6}{1}$, $\frac{12}{1}$).

Hydrophilidae. *Megasternum boletophagus* Marsh ($\frac{2}{1}$, $\frac{6}{1}$, $\frac{7}{1}$, $\frac{10}{2}$).

Scarabaeidae. *Aphodius ater* De G. ($\frac{9}{1}$, $\frac{11}{1}$); *A. contaminatus* Herbst. ($\frac{3}{1}$, $\frac{9}{4}$); *A. fimetarius* L. ($\frac{11}{2}$, $\frac{12}{1}$).

Staphylinidae. *Atheta* (*Homalota*) *analis* Grav. ($\frac{1}{2}$, $\frac{2}{3}$, $\frac{6}{1}$, $\frac{7}{6}$, $\frac{8}{3}$, $\frac{9}{2}$, $\frac{10}{2}$, $\frac{11}{9}$, $\frac{12}{10}$); *A.* (*H.*) *fungi* Grav. ($\frac{1}{3}$, $\frac{2}{2}$, $\frac{3}{4}$, $\frac{6}{2}$, $\frac{7}{3}$, $\frac{12}{9}$); *Tachyporus chrysomelinus* L. ($\frac{1}{3}$, $\frac{3}{6}$, $\frac{11}{1}$, $\frac{12}{2}$); *T. hypnorum* Fab. ($\frac{1}{1}$, $\frac{12}{1}$); *T. humerosus* Erich. ($\frac{10}{1}$, $\frac{11}{1}$, $\frac{12}{3}$); *Tachinus laticollis* Grav. ($\frac{11}{1}$); *T. rufipes* De G. ($\frac{1}{1}$, $\frac{3}{1}$); *Philonthus laminatus* Creutz ($\frac{7}{1}$); *P. varius* Gyll. ($\frac{2}{1}$, $\frac{12}{1}$); *Gabrius* sp. ($\frac{12}{1}$); *Othius melanocephalus* Grav. ($\frac{11}{1}$, $\frac{12}{1}$); *Xantholinus linearis* Oliv. ($\frac{1}{2}$, $\frac{8}{1}$, $\frac{9}{1}$, $\frac{12}{3}$); *Stenus brunnipes* Steph. ($\frac{11}{4}$, $\frac{12}{2}$); *Platystethus arenarius* Fourc. ($\frac{11}{1}$, $\frac{12}{3}$); *Oxytelus sculpturatus* Grav. ($\frac{7}{1}$).

Elateridae. *Agriotes obscurus* L. ($\frac{1}{2}$, $\frac{2}{1}$, $\frac{12}{1}$).

Chrysomelidae. *Longitarsus luridus* Scop. ($\frac{3}{1}$, $\frac{11}{1}$); black var. ($\frac{2}{1}$).

Byrrhidae. *Simplocaria semistriata* Fab. ($\frac{6}{1}$, $\frac{9}{1}$).

Curculionidae. *Apion virens* Herbst. ($\frac{1}{1}$, $\frac{6}{1}$); *Sitones puncticollis* Steph. ($\frac{7}{1}$, $\frac{11}{1}$).

Larvae and pupae.

Carabidae. Sp. ($\frac{10}{1}$).

Scarabaeidae. Sp. ($\frac{6}{2}$, $\frac{11}{3}$).

Staphylinidae. *Tachyporus* ($\frac{7}{1}$, $\frac{10}{1}$); *Quedidus* ($\frac{2}{1}$, $\frac{7}{1}$); *Xantholinus* ($\frac{3}{2}$, $\frac{7}{11}$, $\frac{8}{1}$, $\frac{10}{1}$, $\frac{11}{2}$); other species ($\frac{7}{8}$).

Elateridae. *Agriotes* ($\frac{1}{42}$, $\frac{2}{4}$, $\frac{3}{4}$, $\frac{8}{2}$, $\frac{9}{1}$).

Curculionidae. *Sitones puncticollis* Steph. ($\frac{6}{10}$, $\frac{7}{14}$); other species ($\frac{1}{1}$, $\frac{6}{5}$, $\frac{7}{2}$, $\frac{9}{2}$, $\frac{10}{5}$, $\frac{11}{12}$, $\frac{12}{2}$).

Diptera.

Larvae and pupae.

Mycetophilidae. Sp. ($\frac{1}{129}$, $\frac{2}{26}$, $\frac{6}{2}$, $\frac{10}{85}$, $\frac{11}{63}$).

Bibionidae. *Bibio Johannis* L. ($\frac{1}{14}$, $\frac{2}{49}$, $\frac{3}{10}$); *Bibio* sp. ($\frac{9}{464}$).

Tipulidae. *Tipula* sp. ($\frac{1}{1}$, $\frac{11}{4}$, $\frac{12}{2}$).

Stratiomyidae. *Odontomyia felina* Pz. ($\frac{3}{1}$).

Leptidae. *Leptis* sp. ($\frac{10}{11}$).

Anthomyidae. *Phorbia ignota* Rond. ($\frac{6}{9}$); sp. ($\frac{7}{2}$, $\frac{8}{1}$, $\frac{11}{1}$).

Hymenoptera.

Larvae and pupae.

Tenthredinidae. *Dolerus fissus* Htg. ($\frac{2}{1}$).

Ichneumonidae. *Amblyteles armatorius* Forst. ($\frac{6}{1}$).

Larvae belonging to the following families were found at a greater depth than two inches: *Coleoptera.* Scarabaeidae, 2 to 6 ins. ($\frac{11}{2}$); Curculionidae, 2 to 4 ins. ($\frac{10}{1}$); 2 to 4 ins. ($\frac{41}{1}$), 2 to 6 ins. ($\frac{11}{1}$); family not det. 2 to 6 ins. ($\frac{1}{1}$). *Diptera.* Mycetophilidae, 2 to 6 ins. ($\frac{11}{58}$); family not det. 4 to 8 ins. ($\frac{10}{2}$).

8. ADULT INSECTS ASSOCIATED WITH THE HERBAGE OF THE AREA AND TAKEN BY SWEEPING.

Collembola.

Sminthuridae. *Sminthurus viridis* (Linn.) Lubb. (6, 8, 10).

Rhynchota.

Homoptera—

Cercopidae. *Philaenus spurmarius* L. (6).

Acocephalidae. *Acocephalus nervosus* Schr. (9).

Jassidae. *Cicadula sexnotata* Fall. (6, 7, 9).

Heteroptera—

Capsidae. *Megaloceraea ruficornis* Fourc. (7); *Lygus pratensis* Fab. (7); *Psallus lepidus* Fieb. (6).

Lepidoptera.

Pieridae. *Pieris napi* L. (7); *P. rapae* L. (7); *P. brassicae* L. (7).

Nymphalidae. *Vanessa urticae* L. (8).

Pyralidae. Spp. (7).

Coleoptera.

Carabidae. *Pterosticus vulgaris* L. (7); *Bembidium obtusum* Sturm. (9); *Notiophilus aquaticus* L. (7).

Hydrophilidae. *Cercyon flavipes* Fab. (6); *Megasternum boletophagus* Marsh (9); *Cryptopleurum atomarium* Oliv. (10).

Scarabaeidae. *Aphodius fimetarius* L. (9, 10); *A. fossor* L. (6).

Staphylinidae. *Atheta* (*Homalota*) *analis* Grav. (9); *Tachyporus hypnorum* Fab. (9); *T. humerosus* Erich. (9); *Mycetophagus splendens* Marsh (4); *Quedidus attenuatus* Gyll. (9); *Philonthus varius* Gyll. (4); *P. sordidus* Grav. (6); *Oxytelus sculpturatus* Grav. (10); *O. lacqueatus* Marsh (6).

Nitidulidae. *Meligethes aeneus* Fab. (6); *Brachypterus urticae* Fab. (6, 8).

Telephoridae. *Telephorus nigricans* Müll. (4); *T. bicolor* Fab. (6); *T. flavilabris* Fall. (6).

Chrysomelidae. *Longitarsus luridus* Scop. (8, 9, 10); *Plectrocelis concinna* Marsh (7); *Phyllotreta undulata* Kuts. (9).

Curculionidae. *Apion virens* Herbst. (9, 10); *Phyllobius pyri* L. (4); *P. alneti* F. =*urticae* De G. (4); *Sitones puncticollis* Steph. (9, 10); *Caeliodes quadrimaculatus* L. (6).

Diptera.

Mycetophilidae. Sp. (3, 6).

Bibionidae. *Dilophus febrilis* L. (9); *D. albipennis* Mg. (6); *Bibio Marci* L. (6).

Simulidae. *Simulium latipes* Mg. (10); *S. maculatum* Mg. (6); *Simulium* sp. (7).

Tipulidae. *Tipula oleracea* L. (6, 9); *T. paludosa* Mg. (8); *Pachyrrhina histio* F. (6).

Stratiomyidae. *Beris vallata* Forster (6, 7); *Chloromyia formosa* Scop. (6); *Sargus flavipes* Mg. (8).

Tabanidae. *Haematopota pluvialis* L. (6); *Chrysops caecutiens* L. (6).

Leptidae. *Leptis scolopacea* L. (6); *L. tringaria* L. (7); *Chrysopilus auratus* F. (6).

Empidae. *Empis trigramma* Mg. (6, 7); *Hilara* sp. (7).

Dolichopidae. *Dolichopus ungulatus* L. (6); *D. longitarsus* Stan. (6).

Lonchopteridae. *Lonchoptera lutea* Pz. (9, 10, 12).

Syrphidae. *Liogaster metallina* F. (8); *Platycheirus scutatus* Mg. (6); *Platycheirus* sp. (8); *Syrphus albostriatus* Fln. (8); *S. ribesii* L. (8); *S. balteatus* De G. (8); *Melanostoma mellinum* L. (6, 8); *Syritta pipiens* L. (6); *Eristalis horticola* De G. (6); *E. arbustorum* L. (8).

Sepsidae. *Sepsis cynipsea* L. (6, 7).

Opomyzidae. *Opomyza germinationis* L. (6, 9).

Oscinidae. *Chlorops* spp. (7).

Borboridae. *Borborus geniculatus* Mg. (1, 6); *Borborus* sp. (1).

Cordyluridae. *Scatophaga stercoraria* L. (6, 8, 10).

Anthomyidae. *Spilogaster duplaris* Stien. (9); *S. quadrimaculata* Fln. (10); *Hyetodesia* sp. (6); *Phorbia ignota* Rond. (6, 7); *Hydrophoria ambigua* Fln. (6, 8); *Homolomyia serena* Fln. (7); *Hydrotaea palaestrica* Mg. (6); *Hylemyia strigosa* F. (7); *Hylemyia* sp. (6, 7).

Muscidae. *Morellia hortorum* Fln. (6); *Stomoxys calcitrans* L. (9); *Onesia cognata* Mg. (6); *Mesembrina meridiana* L. (6, 8); *Lucilia caesar* L. (8).

Sarcophagidae. *Sarcophaga carnaria* L. (8); *Graphomyia maculata* Scop. (8).

Tachinidae. Sp. (8).

Hymenoptera.

Tenthredinidae. *Dolerus niger* Klug. (6); *Taxonus glabratus* Thoms. (6); *Selandria serva* Ste. (6, 7).

Cynipidae. *Figites nitens* Hartig (7, 9).

Ichneumonidae. *Atractodes gilvipes* Hilgr. (7); *A. vestalis* Hal. (7); *Mesoleius aulicus* Grav. (7); *Platylabus dimidiatus* Grav. (6); *Phygadeuon fumator* Grav. (7); *P. variabilis* Grav. (7); *Hemiteles tristator* Grav. (7).

Braconidae. *Aspilota nervosa* Hal. (7); *Dacnusa misella* Marsh (7); *D. areolaris* Nees. (9); spp. (7, 9).

Vespidae. *Vespa germanica* Fab. (7, 8).

Apidae. *Andrena cineraria* L. (6); *Nomada alternata* Kirby (6); *Nomada* sp. (6); *Bombus terrestris* L. (7).

Chalcidae. *Tetrastichus* sp. (9); *Gonatocerus* sp. (7); *Eucyrtus* sp. (7); *Eulophus* sp. (6).

Proctotrypidae. *Diapria* sp. (9); *Lagynodes*, probably *L. pallidus* Boh. (8).

9. Noteworthy Species in the Insect Fauna.

Rhynchota.

The most abundant species belonging to this order was *Cicadula sexnotata* Fall. which occurred in very great numbers during the months June to September. *Philaenus spumarius* L. was also abundant. The other species of Rhynchota were only occasionally taken. *Psallus lepidus* Fieb. had probably wandered from one of the ash trees on the border of the field.

Neuroptera.

The only representative of this family was *Sialis lutaria*, which occurred near the ponds.

Lepidoptera.

Few species of Lepidoptera were met with in the field, adults and larvae of Pyralidae being the most numerous. Larvae of *Triphaena pronuba* L. occurred in the soil and a pupa of this species was parasitized by the Ichneumon *Amblyteles armatorius* Forst.

Coleoptera.

The family Staphylinidae was quite the best represented, both in point of species and of actual numbers, the commonest species being *Atheta* (*Homalota*) *analis* Grav. A few species such as *Brachypterus urticae* Fab., *Phyllobius urticae* De G. and *Caeliodes quadrimaculatus* L. occurred especially on or near the patches of *Urtica dioica.*

"Wireworms," the larvae of *Agriotes obscurus* L. occurred very frequently, especially in the rougher parts of the field.

The presence of the Scarabaeidae, both adults and larvae, and of the Hydrophilidae was probably due to the patches of dung about the field owing to its having been grazed by cattle and horses.

Apion virens Herbst. and *Sitones puncticollis* Steph. occurred abundantly in the parts of the field in which clover was present. Larvae and pupae of the latter species were taken at the roots of clover, the larvae of the former probably occurring in the same situation.

The single specimen of *Phyllotreta undulata* Kuts., which was obtained, had probably wandered from one of the fields of swedes in the neighbourhood, the nearest being at the east end of field C (Fig. 1).

Diptera.

Larvae belonging to the family Mycetophilidae were frequently met with in the soil, where they sometimes occurred in masses. In one sample of soil 107 Mycetophilid larvae were met with, in another 58 were found.

Larvae of the family Bibionidae also occurred in large numbers, but not so frequently as was the case with the Mycetophilidae; on one occasion 49 larvae of *Bibio Johannis* L. were found in a single sample of soil, and on another occasion 464 larvae of a species of *Bibio.*

Tipula oleracea L. and *T. paludosa* Mg. were fairly numerous but their larvae were not met with very frequently.

Anthomyidae were numerous, especially in the adult state.

Hymenoptera.

Of the Tenthredinidae which occurred, the most plentiful belonged to the genus *Dolerus. Selandria serva* Ste. also occurred several times.

A fair number of parasitic Hymenoptera were taken, usually in the adult state, a specimen of *Amblyteles armatorius* Forst. was, however, reared from a pupa of *Triphaena pronuba* L.

The following are the hosts which have been recorded for the different species of parasitic Hymenoptera (*vide* Morley 1903–1914):

Atractodes gilvipes Hlgr.; recorded from larvae of *Acidalia marginepunctata* Göze.

Atractodes vestalis Hal.; host not recorded.

Mesoleius aulicus Grav. Bred in Europe from *Nematus fulvus, Selandria ovata, Cladius viminalis, Lophyrus pini* L.

Platylabus dimidiatus Grav. Bred from *Depressaria heracleana* and *D. depressella* on the Continent. In this country it has been bred from *Melanippe fluctuata* and *M. montanata.*

Phygadeuon fumator Grav. Bred from *Mamestra brassicae,* probably preys mainly on Anthomyidae.

Phygadeuon variabilis Grav. Reared from Dipterous (probably Tachinid) pupae.

Hemiteles tristator Grav. Has been bred from *Pieris brassicae* and *Limneria* cocoons among the eggs of *Epeira diademata, Fumea intermediella* and *Solenobia triquetrella.*

The Braconid *Aspilota nervosa* Hal. is stated to be parasitic on *Homalomyia (Fannia) canicularis.*

A nest of *Vespa germanica* Fab. occurred on the bank of one of the ponds on the west of the field, and individuals from this and other nests in the neighbourhood were frequently met with in the field.

A number of burrows of *Andrena cineraria* L. occurred in a colony on a small smooth area of bare soil between two of the ponds. These burrows were found in the autumn to contain larvae, adults of both sexes, and other larvae which probably belonged to a parasitic species of *Nomada*, these bees having been seen in the neighbourhood of the burrows during the summer.

10. DISTRIBUTION IN DEPTH.

Relatively few insects, and those all in the larval state, were found at a greater depth than two inches, and none deeper than six inches.

This may be partly due to the fact that the soil was very compact owing to the field having been a permanent pasture for many years. The grass roots, although they formed a solid turf at the surface, did not descend to any depth, as the predominant grasses of the field were shallow-rooted species, and although there was a certain amount of organic matter below the two inch level, there was very little below the six inch level. Even when the ground was covered with three or four inches of snow the insects did not appear to have descended to any greater depth than usual, and when, during a period of hard frost the ground was frozen to a depth of about four inches, it did not appear to cause any change in the depth to which the insects penetrated.

The latter depth in any given area is probably controlled by four factors: depth to which their particular food occurs, aëration, moisture and temperature of the soil. In the present instance the food of both carnivorous and vegetarian forms depended ultimately on the presence of organic matter, either living plants or their decaying remains, this material, as has been noted above, only being present, except in a very small proportion, in the upper six inches, and particularly in the upper two inches.

Owing to the soil not having been disturbed for a considerable time, it had become very much compressed, and consequently the aëration of the soil would be poor, and again, owing to the very stiff subsoil, the rain was not able to drain away readily, in some parts of the field even forming pools on the surface.

As has been mentioned above, the difference in temperature between the upper and lower levels of the soil appeared to have little effect on the insects.

Thus the first three conditions were distinctly unfavourable to deep penetration of the soil by the insects in this case, while the fourth condition was found to have little effect on the depth to which insects descended.

Of the four factors given above, the first, the occurrence of the particular food required by the insect, is largely controlled by the flora of the area, while the second and third, aëration and moisture respectively, are largely controlled by the texture and composition of the soil, which in turn influences the flora. Other factors the influence of which on the insect fauna must be considered are light, wind, rainfall, atmospheric pressure, altitude, exposure and slope. In the present instance these factors do not require to be considered in detail as they would be practically uniform over the district of which the area under observation was selected as being typical.

11. DISCUSSION OF PREVIOUS WORK.

It is noticeable that in this investigation many fewer species were met with than were recorded by Cameron (1917) in his investigation in the same district. This difference is largely accounted for by the fact that in the present instance care was taken to select an environment as uniform as possible, in which little invasion by insects not belonging to the area under observation would occur. In the former case the area was of a very composite nature and included a small wood and fields under various crops. In addition, his two pastures were much "rougher" than that now dealt with, containing a much larger proportion of weeds, and patches of long grass. In his earlier work (1913), Cameron also dealt with an area which was not uniform, and included a field which had been artificially levelled and a small orchard, with several decaying logs and vegetable refuse.

In both the above cases there was a much greater variety of food available, and consequently many more species of insects were present, and there was also considerable variation in the texture of the soil in different parts of the area.

It is rather remarkable that a greater number of individuals should have been found in this field than in either of the fields in the same district examined by Cameron, which are marked Lc and N on the map.

This is possibly due, in the case of "Glover's Meadow," to the absence of dung from the field, as that substance attracts many species, including the species of *Bibio*, to which the high figure obtained in the present area was partly due. With the "Alluvial Pasture," the difference may be due to its tendency to be marshy throughout the year, which condition is unfavourable to soil insects.

12. CENSUS OF SOIL INSECTS.

During the investigation twenty-nine samples, each with a superficial area of 100 square inches, were examined, and a total of 1658 insects were obtained. From this figure the total number of insects in an acre of the field works out at 3,586,088, which is probably somewhat below the actual number, as with small insects like *Collembola* and *Thysanoptera*, it is difficult to be sure of securing every specimen, and a proportion of the more active forms of the other families probably effect their escape during the removal of the soil.

The numbers of the different orders were: *Collembola*, 566,680; *Rhynchota*, 15,140; *Thysanoptera*, 43,258; *Lepidoptera*, 15,140; *Coleoptera*, 744,038; *Diptera*, 2,193,180; *Hymenoptera*, 8652.

The figure for *Diptera* is considerably increased by the finding on one occasion of 464 larvae in a sample, but about 50 larvae were not infrequently met with in a sample of soil.

Among notably injurious species the numbers per acre work out as follows: *Agriotes*, larvae 114,634, adults 8652; larvae and pupae of *Triphaena pronuba* L. 4326; larvae of *Tipula oleracea* and *T. paludosa* 19,466.

The numbers of insects per acre found by Cameron, as calculated from the figures he gives, are 835,560 for "Glover's Meadow," and 1,537,046 for the "Alluvial Pasture." M'Atee, working near Washington, U.S.A., calculated that on an acre of forest floor there were 1,216,880 animals belonging to *Insecta*, *Arachnida* and other *Arthropoda*, *Annelida* and *Gastropoda*; similarly in an acre of meadow land in the same locality he calculated that there were 13,654,710 animals.

As this figure includes *Arachnida* and other *Arthropoda*, *Annelida* and *Gastropoda*, it cannot be compared with the figure obtained in the present instance.

13. SUMMARY.

1. An area was chosen which was as typical as possible of the permanent pasture fields of the district, and in which invasion by insects not belonging to the area would be reduced to a minimum.

2. In order to define the characters of the area under consideration as clearly as possible, chemical, mechanical and botanical analyses were carried out.

3. Insects, largely in immature forms, were obtained by examining samples of soil from various parts of the area, and in addition many adults were obtained by sweeping the herbage with a net. The latter method produced also some invading forms which did not belong to the area.

4. The factors influencing the distribution by depth of the insects in the soil were in this case chiefly occurrence of food, aëration, and moisture, and the result of these influences was that the insects seldom penetrated even as deep as six inches, the vast majority of specimens being found at a depth not greater than two inches.

5. The census of insects actually found in the samples of soil gave an insect population of 3,586,088 per acre. The family best represented in number of individuals was the Bibionidae, species of which made up 32·4 per cent. of the total number of soil insects. The next in number were the Mycetophilidae 16·7 per cent., and the Staphylinidae 12·2 per cent. With regard to number of species occurring in the soil, the Coleoptera, with 29 species, was the best represented order.

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"DAMPING OFF" AND "FOOT ROT" OF TOMATO SEEDLINGS

By W. F. BEWLEY,

Experimental and Research Station, Cheshunt.

"Damping off" is a term commonly used by nurserymen to describe the death of very young seedlings. In the seed-boxes, the young seedlings are attacked at the base, and the rapid collapse of the stem tissues at this point causes the seedlings to fall over.

"Foot Rot" is the term applied when the young plants are attacked at a later date. In this case the seedlings grow strongly in the seed-boxes, but are attacked after "potting up" or even after "planting out" in the houses. As in the case of "damping off," the base of the stem is attacked, and these tissues collapse causing the plant to fall over.

Generally the highest death rate has occurred after periods of watering, and this has led growers to draw a close connection between the disease and damping, and has given rise to the name "damping off." Properly speaking, the term applies to a fatal disease set up through the agency of parasitic fungi, but it is often made to embrace the wilting of seedlings caused by some injurious chemical or physical factor in the soil. These latter causes of death are of somewhat rare occurrence, and when they do take place may usually be traced to carelessness on the part of the workman.

Cresylic acid, which is extensively used in the winter for sterilising the wood-work, staging and soil itself in the glass houses, has occasionally been known to produce a wilt of young plants, when the proper precautions necessary in such sterilisation have been disregarded. In one instance, an insufficient time had elapsed between sterilising the propagating benches and the raising of seedlings upon them. The result was that the seedlings were stunted in growth and turned a blue-green colour; many were so scorched in the stem that they fell over and had all the appearances of "damped off" seedlings.

In another instance a quantity of undiluted cresylic acid had been upset in one part of a house by a workman, who omitted to report the accident. In due course the house was planted, and, while the greater number of the individuals grew quite healthily, it was observed that in one spot all the plants died. These showed all the symptoms usually associated with the disease caused by *Phytophthora cryptogea*, but examination showed that no pathogenic organisms were present in the diseased tissues. Further inquiries led to the knowledge that the area containing the dead plants was that in which the cresylic acid had been upset.

The deleterious effect which ammonia has upon plant growth is frequently observed, and in no place, perhaps, is the result so marked as in the glass houses where high temperatures prevail. In the early stages of the tomato crop examples can frequently be seen of "damping off" effects produced through the rapid diffusion of ammonia from soil which contains dung not sufficiently matured.

The investigations to be described have been directed towards the congeries of diseases caused by pathogenic fungi.

Sources of Infection.

At the outset one is faced by a number of possible sources of infection all of which require careful investigation if complete control of the disease is to be effected. The seeds themselves, the seed-boxes and soil, the stages upon which the boxes rest, and the water used in cultivation are all possible sources of infection.

The Seeds.

It is well known that the coverings of many seeds carry fungus spores which germinate in the soil and destroy the young root as it emerges. The tomato seed is especially suitable for carrying spores, for its testa, being provided with long hairs, easily holds small particles.

Apart from this, the method usually employed by the practical man for the extraction of seeds from the fruits, increases the suspicion as to the purity of the seed. Certainly the best fruits are chosen for the purpose, but the subsequent treatment renders the seed liable to a great deal of contamination. The fruits are first divided in halves and the seeds with the mucilage which surrounds them are cut out into a pail. In order to facilitate the removal of the mucilage, the whole mass is allowed to ferment and soon becomes a mass of putrefaction, forming a pabulum for all kinds of fungi and bacteria. This part of the process is perhaps the most open to criticism because of the opportunity it offers for the rapid growth of any organism, pathogenic or otherwise, that may be carried to the fermenting matter. The length of time the mucilage and seeds remain in this state varies considerably, but experiment shows that three or four days are sufficient to destroy the mucilage and allow of its easy removal. It is unnecessary and undesirable to allow too long a time for this preliminary rotting of the mucilage. After the fermentation the seed is washed and dried. To reduce the possibility of infection the extraction should be carried out under hygienic conditions, and away from the vicinity of the growing plant where there is danger of contamination from fungus spores in the air. The fruit should be wiped with a rag containing a little lysol or cresylic acid or sprayed with a 2 per cent. solution of formaldehyde in order to sterilise the outside. It must then be well washed, dried and carried to some clean shed or room, where the air is still, and there the seed should be removed.

An examination of many different samples of seed has shown that they carry on their testas a very varied fungus flora, but so far we have been unable to find any active parasites. This, of course, does not prove that tomato seeds never carry destructive organisms but it indicates that such is a rare occurrence. The hairiness of the seed coat and the presence of many fungus spores point to the fact that disease organisms may be carried also. In this connection it is interesting to note that I. Massee[1] has described the presence of hibernating mycelium of *Macrosporium solani* underneath the seed coat in samples of tomato seeds she examined. It is advisable to test all bought seed in a trial box under sterile conditions some time before the general sowing. Seed suspected of impurity should be sterilised. Home produced seed should be free from disease, provided it is derived from the best fruits and has been extracted under hygienic conditions.

Seed-boxes and Pots.

General observation and experimental work show that the disease organisms are carried over from one season to the next by seed-boxes and pots. Discolouration and destruction of plant roots has frequently been traced to some crack or crevice in the pot or box which has harboured the resting spores of the fungus.

The Soil.

The organisms producing "damping off," like many others, spend part of their existence in the living plant and the rest in hibernation over the winter in the decomposing soil humus. So far as we have been able to determine, "damping off" of tomato seedlings is produced by three different organisms which appear to be *Phytophthora terrestria* (Sherbakoff)[1], *Ph. cryptogea* (Pethybridge)[2] and *Rhizoctonia solani* (Kuhn) Duggar[3] respectively, though precise identification is not possible until comparisons of pure cultures are completed. *Ph. terrestria* also produces "buck-eye" rot of tomato fruits, stem rot and "foot rot" of the tomato, and stem rot of the lupin. *Ph. cryptogea* has been described[4] as producing "foot rot" of the tomato and aster, and not infrequently it is very destructive to antirrhinums and lupins. *Rhizoctonia solani* is regarded as a universal soil organism, which attacks young plants.

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[1] Massee, I. *Kew Bulletin*, No. 4, 1914.

The Water Supply

Observations in nurseries where epidemics of "damping off" and "foot rot" have been in progress led us to suspect the water as being an important source of infection. Preliminary experiments on seedlings on which water suspected of contamination had been used confirmed this suspicion. We have therefore undertaken an extensive analysis of nursery waters in the Lea Valley to ascertain what organisms pathogenic to the tomato they contain. The results, which will be given in a further communication, show that while some waters are practically free from pathogenic organisms, others contain the spores of many tomato parasites. The problem of pure water supply is exceedingly important and requires very careful investigation. One important and obvious precaution is to avoid all danger of polluting the well by surface drainage from the nursery, or any allotment, garden, etc.

EXPERIMENTAL.

An examination was made of diseased seedlings from various nurseries in the district. The pathogenic organisms were identified, isolated in pure culture and tested for pathogenicity.

The dominating pathogen, here called *Phytophthora* "*A*," appeared to be identical with *Phytophthora terrestria* described by Sherbakoff[5] in America as producing "buck-eye" rot of tomato fruits and stem rot of citrus trees and lupins, and is probably identical with *Ph. parasitica* described by Dastur[1] in India as attacking castor bean plants. Nearly equal in importance is *Phytophthora "B,"* probably *Ph. cryptogea*, which has been described by Pethybridge and Lafferty[2] as producing a "foot rot" of the tomato plant. In a few cases *Rhizoctonia solani* was the causative organism. Samples of soil were then obtained from several nurserymen and tested for their power to produce "damping off." Throughout the whole of our experiments sterile seed-boxes (14″ × 9″ × 2″), soil at the rate of five pounds per box, disease-free seed selected by sifting, and sterile water were used. Seed-boxes were "made up" from the soil samples and seeds were sown in the usual manner. Where "damping off" occurred, one or more of the above mentioned fungi was invariably found.

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[1] Sherbakoff, C. D. *Phytopath.* vol. VII, No. 2, 1917.

[2] Pethybridge, G. H. and Lafferty, H. A. *Sci. Proc. Roy. Dubl. Soc.*, vol. XV (N.S.), No. 35, 1919.

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[4] Pethybridge, G. H. and Lafferty, H. A., *loc. cit.* Spinks, G. T. *Ann. Rept. Agr. and Hort. Res. Sta., Long Ashton, Bristol*, 1917. Robinson, W. *Ann. App. Biol.* vol. II, 1915.

[5] Sherbakoff, C. D. *Loc. cit.*

Table I.

Soil	No. of boxes	Parasitic organism
From trade nurseries	10	Phytophthora "A"
,, ,,	3	Phytophthora "A" and *Rhizoctonia solani*
,, ,,	5	Phytophthora "B" and *Rhizoctonia solani*
,, ,,	6	Phytophthora "B"
New turf	3	No disease
Old turf (station)	3	,,
,, (trade nursery)	3	Phytophthora "A"
Old cucumber borders	3	No disease
,, ,,	3	Phytophthora "A"
Tomato house (station)	3	,,
Tomato house sweepings (station)	3	,,
Sandy subsoil	3	No disease
Baked soil	3	,,
Steamed soil	3	,,

Preparation of infected soil to be tested.

The naturally infected soil used for the whole of the experiments described in this paper was obtained from a nursery where "damping off" had been very destructive. The soil was placed under cover on a flat surface and spread out in a layer of some six inches deep. It was thoroughly broken up and mixed with a spade. Next it was divided into eight small heaps and each heap thoroughly worked in turn. Heap 1 was then added to heap 2 and the combined heap well mixed. Heap 3 was then added to heaps 1 and 2 combined and so on until the whole soil was worked into one heap.

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[1] Dastur, J. F. *Memrs. Dept. Agr. India, Bot. Series*, vol. v, No. 4, 1913.

[2] Pethybridge, G. H. and Lafferty, H. A. *Loc. cit.*

Probable error of the average percentage of diseased seedlings per box.

Twelve boxes were each given 5 lbs. of infected soil per box, soaked with water, sown with 100 seeds selected by sieving, and covered with a layer of soil. The percentage germination of the seeds sown and the percentage diseased of those which germinated was ascertained. The seedlings were removed as soon as they became diseased in order to eliminate the factor of lateral spread, and each experiment was brought to a close at the end of 14 days.

From the percentages set down below the probable error of the mean of twelve results was calculated.

% diseased per box	Difference between each result and the mean	(Difference)^2
42	−2·8	7·84
43	−1·8	3·24
44	−0·8	0·64
44	−0·8	0·64
44	−0·8	0·64
45	+0·2	0·04
45	+0·2	0·04
45	+0·2	0·04
45	+0·2	0·04
46	+1·2	1·44
47	+2·2	4·84
48	+3·2	10·24
Mean = 44·8		Sum = 29·88

$$\text{Probable error of each result} = 0{\cdot}67\sqrt{\frac{29{\cdot}88}{11}} = \pm 1{\cdot}102.$$

$$\text{Probable error of the mean} = \frac{\pm 1{\cdot}102}{\sqrt{12}} = \pm 0{\cdot}29.$$

From the above results it will be seen that the percentage of diseased seedlings per box varied from 42 to 48, while the mean was 44·8. This makes the probable error of each result 1·1 and the probable error of the mean 0·29. This result is typical of the results obtained from the whole of the experiments in this paper. In no case was there a wide divergence from the mean and the mean can therefore be taken as an adequate measure of the effect of the particular "limiting factor" under investigation.

Experiments were set up to test the effect of different methods of making up the seed boxes upon the incidence of the disease. The standard method was to weigh out 5 lbs. of soil into each box. Then the soil was compacted by means of a builder's board, soaked with water, 100 seeds per box were sown and covered with a thin layer of sterile soil. In certain instances, however, sand, lime or charcoal was used in place of the sterilised soil. In other cases a layer of sand, lime or charcoal was put on over the sterile soil, and in still other cases the soil was mixed with different proportions of sand, lime or charcoal. A parallel set of experiments was set up at the same time, using sterilised soil. Diseased seedlings were removed from the boxes as soon as they were attacked in order to eliminate the factor of superficial spreading of the disease. The results of these experiments are shown in Table II.

In the above experiments the soil sample, its weight, the sterility of the seed-boxes, the seeds, the temperature, the barometric pressure, the quality and quantity of the light, and the quantity of sterile water given to each box were constant factors. The limiting factors were solely those indicated in the above table. An examination of the percentage germination columns shows that the difference between the lowest percentage germination and the highest is fairly constant and the remainder of the results are symmetrically placed about the mean. The percentage diseased seedlings showed a similar arrangement. This further indicates that the average percentage results can be taken as accurate measure of the experiment in question.

A covering of sand, charcoal or lime either alone or above a covering of sterile soil produces only a small increase or decrease in the percentage of diseased seedlings per box. Charcoal has no effect, when put on as a covering to the seeds. Sand reduced the percentage diseased by 20 per cent., while lime increased it by 25 per cent. Five per cent. of charcoal added to the soil has a distinctly beneficial effect, for, besides reducing the percentage of diseased seedlings by 25 per cent., it produced a fine crop of sturdy dark green seedlings. A further increase in the amount of charcoal added is not advisable, for it only increased the difficulty of keeping the soil at an even degree of moisture. Certainly a decrease in the percentage of diseased seedlings is induced but this is obviously caused by the increased proportion of sterile particles in the soil. In the case of lime, whether it is added as a covering to the seeds or mixed with the soil itself it increased the percentage of diseased seedlings by nearly 50 per cent., and appears actually harmful. This is in agreement with the fact that the parasitic organisms grow best in a neutral medium.

The relation of the closeness of sowing to the spread of the disease.

In order to ascertain the correct closeness to sow the seeds, and the effect of closeness of sowing upon the incidence of the disease the

Table II

Treatment	No. of boxes	Infected soil						Sterilised soil			
		Aver. % germ.	Lowest % germ.	Highest % germ.	Aver. % diseased	Lowest % diseased	Highest % diseased	Aver. % germ.	Lowest % germ.	Highest % germ.	Aver. % diseased
Seed covered with ¼″ sand	12	95	92	97	36	33	37	95	92	97	None
,, ,, ¼″ charcoal	12	97	93	99	47	45	48	96	93	99	,,
,, ,, ¼″ lime	12	96	93	98	66	64	68	95	94	97	,,
,, ,, ¼″ sterilised soil	12	96	94	99	45	42	49	97	95	100	,,
,, ,, ¼″ infected soil	12	97	93	99	47	43	50	—	—	—	,,
Seed covered with ¼″ sterile soil and then ¼″ sand	12	95	92	96	39	36	41	96	94	98	,,
,, ,, ,, ¼″ charcoal ...	12	94	90	96	45	43	48	97	95	98	,,
,, ,, ,, ¼″ lime	12	97	92	100	60	58	61	96	94	97	,,
,, ,, ,, ¼″ lime and charcoal	12	96	93	99	53	51	54	97	96	99	,,
Seed covered with ¼″ sand then ¼″ charcoal	12	95	92	97	40	37	42	96	95	97	,,
95 % soil + 5 % charcoal	12	97	92	100	33	29	35	97	96	99	,,
75 % ,, +25 % ,, ...	12	96	92	98	25	22	28	97	95	98	,,
50 % ,, +50 % ,, ...	12	94	91	98	20	18	25	95	92	98	,,
95 % ,, + 5 % lime	12	98	93	100	69	66	71	97	94	99	,,
75 % ,, +25 % ,, ...	12	95	92	99	51	49	54	96	95	98	,,
90 % ,, + 5 % lime + 5 % charcoal	12	97	93	99	37	34	39	96	94	97	,,

following experiments were made. Seeds were sown in infected soils in thickness varying from 600 to 25 seeds per box, in sets of four boxes at each degree of thickness. In half the boxes the seedlings were removed, as they were attacked, to eliminate the factor of spread. The remainder were untouched and gave some indication as to the rate of superficial spread of the fungus. The results obtained are shown in Table III.

Table III.

No. of seeds per box	Average % diseased seedlings removed when attacked	Average % diseased seedlings not removed
600	51	100
300	45	100
200	49	100
100	42	78
50	37	46
25	35	41

The second column of the above table shows the uniform results obtained when the seedlings were removed as they were attacked. It indicates that the number of seedlings primarily attacked depends upon the number of disease centres in the soil and not upon the closeness of sowing, when the factor of superficial spread of the organisms is eliminated. The third column where the fungi were allowed to spread is of great practical interest, and shows that the rate of spread of the organism is more rapid, where the seeds are closely sown, than where they are thinly sown. In the closer sowings the density of the plants increases the film of water adhering to the seedlings and offers a ready means of spreading the disease through the box.

Sowing above fifty to the box should be avoided as this materially assists the disease.

The relation of the time and method of watering to the incidence of the disease.

Boxes were "made up" in the usual way, using 5 lbs. of infected soil from the stock heap, sowing 100 seeds per box and removing the seedlings as they became diseased. As soon as the seedlings appeared, the glass covers were removed and the different methods of watering were commenced. For top watering in the morning, midday and evening, 200 c.c. of sterile water were given to each box on every alternate day. For bottom watering the boxes were placed for five minutes each in a zinc tray filled half an inch deep with water. One set of boxes was placed on damp earth in a tray on the staging and received no direct watering after their first soaking preparatory to sowing. The soil upon which they rested was kept moist, and the seed-boxes obtained their moisture by capillary attraction. The results of these experiments are shown in Table IV.

Table IV.

Method of watering	No. of boxes	No. of seeds per box	Average % diseased
Top watering—evening	12	100	42
,, mid-day	12	,,	54
,, morning	12	,,	45
Stood continuously in tray of water	12	,,	73
Bottom watering, when necessary	12	,,	27
Placed on damp earth	12	,,	12

The foregoing experiments indicate that either morning or evening watering is preferable to midday watering and that bottom watering is preferable to top watering. The high percentage of diseased seedlings obtained where the boxes were stood continuously in water emphasises the intimate relation between the rapid progress of the disease and a high water content of the soil. Excellent results were obtained by placing the boxes upon damp earth and allowing them no water except what they obtained by capillary attraction from the earth below. Under such conditions the percentage of diseased seedlings was reduced from 45 per cent. to 12 per cent.

The effect of potash, phosphates and nitrogen upon the incidence of the disease.

In order to test the effect of different manurial treatments upon the incidence of "damping off," 0·5 per cent. of sulphate of potash, nitrate of soda and superphosphate was added to the soil either singly or in different combinations.

100 seeds per box were sown, covered in the usual way, and the seedlings removed as soon as they became diseased.

Table V.

Treatment	No. of boxes	No. of seeds per box	Average % diseased
11 gms. K_2SO_4 per 5 lbs. soil	10	100	11
,, $NaNO_3$,, ,,	10	100	49
,, super. ,, ,,	10	100	43
11 gms. K_2SO_4 and 11 gms. $NaNO_3$ per 5 lbs. soil	10	100	45
,, ,, ,, super. ,, ,,	10	100	29
,, $NaNO_3$ and 11 gms. super. ,, ,,	10	100	51
Control	10	100	45

The results tabulated above indicate that superphosphate and nitrate of soda have but little effect upon the disease. On the other hand a dressing of 11 gms. of sulphate of potash per 5 lbs. of soil, brought about a considerable reduction in the average of diseased seedlings; this result serving once more to emphasise the power of suitable dressings of potash to restrict fungus diseases.

Fungicides.

In these tests the boxes were made up in the usual way, using infected soil; 100 seeds per box were sown and covered; the fungicidal solutions in the quantities shown in Table VI were then applied from a copper sprayer. The boxes were left until the seeds germinated, when the percentage germination and the percentage diseased seedlings were determined. Each diseased seedling was removed as it fell over.

Table VI.

Treatment	No. of boxes	Average germination	Average % diseased seedlings
Control	6	97	45
400 c.c. 2% solution of copper sulphate	6	9	25
,, 1% ,, ,,	6	37	43
,, ½% ,, ,,	6	94	41
,, 2–3–50 Bordeaux mixture	6	95	37
,, 4–4–50 ,,	6	93	28
,, 4–4–100 ,,	6	97	39
,, 2–3–50 Burgundy mixture	6	92	39
,, 1 in 25 formaldehyde solution	6	0	—
,, 1 in 50 ,,	6	0	—
,, 1 in 100 ,,	6	93	40
,, 1 in 250 ,,	6	95	47
,, 0·75% solution of sodium fluoride	6	25	7
,, 0·5 % ,, ,,	6	98	23
,, 0·1 % ,, ,,	6	96	43
,, 0·5 % solution of barium polysulphide	6	93	47
,, 0·01% ,, phenol	6	95	45
¼ oz. ,, sodium chloride (sprinkled over the soil)	6	97	39

The results obtained indicate that none of the solutions tested are able to control the disease, without injury to the plants.

Control of the disease by soil sterilisation.

Sterilisation of the soil by heat or formaldehyde has proved the most effective method of controlling "damping off."

Sterilisation by steam.

Twelve boxes of naturally infected soil and twelve of inoculated soil were made, six of each being steamed for two hours and the remaining twelve being left untreated to serve as controls. After cooling the whole twenty-four boxes were sown in the usual manner, 100 seeds per box, and the seedlings removed as soon as they became diseased. The seedlings in the steamed soil were perfectly healthy, while the unsteamed controls showed an average of 47 per cent. of diseased plants in each box. Apart from the control of the disease the steamed soil gave much the best type of seedlings. They were more healthy and vigorous and showed better root development than those in the untreated soils. The steaming also killed all the weeds.

Sterilisation by baking gave similar results.

Sterilisation by formaldehyde.

Formaldehyde has long been recommended as a soil fungicide. The soil in the boxes was saturated with different concentrations of formaldehyde; it was then covered for 48 hours to allow the vapours to act. After this time had elapsed the covers were removed and the soil allowed to dry, and seeds were then sown in the usual way. The results are shown in Table VII.

Table VII.

Strength of sterilising solution	Average number of diseased seedlings per box
1 c.c. 40% formaldehyde per 200 c.c. water	44
1 ,, ,, 150 ,,	45
1 ,, ,, 100 ,,	42
1 ,, ,, 75 ,,	37
1 ,, ,, 50 ,,	0
1 ,, ,, 25 ,,	0
1 ,, ,, 10 ,,	0

Our results show that all strengths of formaldehyde solutions from 2 per cent. upwards are effective in soil sterilisation, but the weaker solutions are not sufficiently strong to completely sterilise the soil. Our untreated controls in the above experiments gave an average of 48 per cent. diseased seedlings. Further experiments showed that complete sterilisation of the diseased soil could be carried out by the following method. A formaldehyde solution is made by adding one ounce of commercial formalin (40 per cent. formaldehyde) to 2½ pints of water (*i.e.* 1 in 50). The soil is saturated with this solution, covered with glass for 48 hours, and allowed to stand uncovered for 10 days to make sure all the formaldehyde has evaporated. The seed is then sown in the usual manner. So long as the water is not infected this treatment will ensure a healthy batch of seedlings.

The Seed-box as a Carrier of Disease.

Twenty-four boxes in which "damping off" had been very severe were used. Twelve were left untreated as controls and the remaining twelve were soaked for ten minutes in a 2 per cent. solution of formalin contained in a tub. They were then placed in a heap and covered with sacking for 48 hours in order to allow the vapours of the formaldehyde to act upon the fungi present in the boxes. After this time the sacking was removed and the boxes allowed to dry. All the boxes both treated and untreated were then made up with sterilised soil, sown with sterilised seed, watered with sterile water and placed on sterilised glass plates in the greenhouse. The plants grown in the sterilised boxes were perfectly healthy and showed no signs of "damping off," while eleven boxes out of twelve untreated showed an average of 14 per cent. diseased seedlings.

The results of this experiment, which are given in Table VIII, show that seed-boxes carry the infection from one season to another.

Table VIII.

Date	Untreated boxes	Treated boxes
7. 8.19	Seed sown	Seed sown
20. 8.19	One box showed disease	All boxes with healthy plants
30. 8.19	Five boxes showed disease	,, ,, ,,
7. 9.19	Nine boxes showed disease	,, ,, ,,
23. 9.19	Eleven boxes showed disease	Two diseased seedlings in one box
7.10.19	Eleven boxes showed disease One box with healthy plants	,, ,, ,,

The Pot as a Carrier of Disease.

Twelve pots which had previously contained plants attacked by "foot-rot" were obtained from a nursery. Six were treated with a 2 per cent. solution of formalin in the same manner as the boxes in the previous experiment, while six were left untreated to serve as controls. In four of the six untreated pots the plants developed "foot-rot," while in all the six treated pots the plants remained perfectly healthy.

Sterilisation by formaldehyde of the soil in heaps.

The soil used in the experiment was naturally infected soil obtained from a nursery; and when tested was found to produce the disease quite readily. Two heaps were made, each of 60 lbs.; one was left untreated and into the other was gradually worked 2 gallons of a 2 per cent. solution of formalin, the whole being thoroughly mixed with a spade. It was then covered with sacking for 48 hours, after which the sacking was removed and the heap spread out and allowed to dry. Fourteen days after treatment, nine boxes and six pots were filled from each heap. The boxes were sown with sterile seed and the pots planted with young healthy seedlings reared in sterilised soil. In each case sterile water was used for watering. The treated soil produced plants free from disease, while the untreated soils in the nine boxes showed an average of 48 per cent. of diseased plants and five pots out of six contained plants affected with "foot-rot."

The time after treatment at which it is safe to sow.

Twenty-four boxes were made up with naturally infected soil. Twenty were treated with a 2 per cent. solution of formalin, covered, and sown in pairs on successive days. One hundred seeds were sown per box, and the infected seedlings were removed as soon as they were attacked.

Table IX.

Time of sowing	Percentage germination	Percentage diseased
On removing covers	49	0
1 day after	57	0
2 days after	69	0
3 ,,	51	0
4 ,,	100	0
5 ,,	97	0
6 ,,	98	0
7 ,,	93	0
10 ,,	94	0
14 ,,	98	0

The untreated controls showed an average of 44 per cent. diseased seedlings per box.

In this experiment it was safe to sow from four to seven days after treatment, but in practice it is better to allow a fortnight interval for the vapours to pass completely out of the soil.

Treatment after disease has appeared.

Numerous attempts have been made to stop the disease once it has become established in the seed-box. In our experiments, the diseased seedlings were removed and the remainder were sprayed with different fungicides or treated as indicated in Table X. The only treatments that resulted in an appreciable reduction of the disease were those of copper sulphate with lime, and formaldehyde with ammonia. Ten parts of dry powdered lime obtained from freshly slaked lime, and one part of copper sulphate were ground to a fine powder and thoroughly mixed. After passing through a fine sieve the mixture was sprinkled thinly over the soil. By this treatment only 7 per cent. of diseased seedlings resulted.

When formaldehyde and ammonia are mixed an impure solution of hexamethylene tetramine is produced. In the tests, commercial formalin (containing 40 per cent. formaldehyde) was added to a strong solution of ammonia, ·880, in the correct proportions to produce a 40 per cent. solution of hexamethylene tetramine. This was diluted to various concentrations, and 400 c.c. watered on the boxes. The most suitable strength to use proved to be a 0·5 per cent. solution. By its application the percentage of diseased seedlings was reduced to 11. Experiments with older plants "potted up" in diseased soil showed similar results.

Table X.

Treatment			Average % diseased
Compound used		Quantity per box	
Mixture of equal parts of charcoal and lime sprinkled over the soil		¾ oz. per sq. ft.	44
10 parts lime and 1 part copper sulphate sprinkled over the soil		,,	7
Sodium fluoride	(0·5% solution)	400 c.c.	43
,,	(0·75% solution)	,,	Injured seedlings
Formaldehyde	(1% solution)	,,	Killed seedlings
,,	(0·5% solution)	,,	34
,,	(0·13% solution)	,,	43
Sodium nitrate	(0·5% solution)	,,	45
Sulphate of potash	(0·5% solution)	,,	32
Sulphuric acid	(1% solution)	,,	Killed seedlings
,,	(0·25% solution)	,,	,,
,,	(0·125% solution)	,,	42
,,	(0·05% solution)	,,	44
Citric acid	(0·5% solution)	,,	40
,,	(1% solution)	,,	41
,,	(2% solution)	,,	43
Hexamethylene tetramine	(5% solution)	,,	Killed seedlings
,,	(1% solution)	,,	,,
,,	(0·5% solution)	,,	11

CULTURAL METHODS OF CONTROL.

The control measures first described, namely soil sterilisation, are those of prevention and cannot be applied after the seed is sown.

It is clear that a certain amount of infection comes from the use of contaminated water, and in nurseries where this has been proved to be the case, it is highly important to obtain a clean water supply.

If the disease has started when the plants are growing, the application of a mixture of 10 parts of lime and 1 part of copper sulphate, put on the soil at the rate of $\frac{3}{4}$ oz. per square foot, has been found to be useful in keeping down the disease. The use of hexamethylene tetramine shows promising results, and further work on this compound is in progress.

The Moisture Factor.

A relatively high percentage of moisture in the soil and the air favours the rapid spread of the "damping off" organism. Careful regulation of the watering, so as to keep the seed-boxes uniformly moist and good ventilation of the propagating houses to dry out the surface soil, will produce the best moisture conditions for checking the disease.

Temperature.

The optimum temperature for growth of *Ph. terrestria* = *Ph. parasitica* is about 30° C. (86° F.), and that of *Ph. cryptogea* and *Rhizoctonia* about 25° C. (77° F.). Below 12° C. (54° F.) the growth of all three is very slow. When the disease has started among the plants, the grower should therefore endeavour to keep the temperature as low as possible without impairing the health of his crop.

Further work is in progress upon the physiological relations of the disease organisms to their environment, and upon their reaction to certain chemical compounds; also upon the method of cleansing contaminated water.

The author takes pleasure in thanking Mr W. B. Brierley of the Rothamsted Experimental Station for the many helpful suggestions and criticisms he has so kindly given him.

CONCLUSIONS

1. "Damping off" of tomato seedlings is a communicable disease due to a group of pathogenic organisms, particularly species of the genus Phytophthora.

2. The organisms do not occur in all soils but exist as a definite infection in some.

3. Infection of the seedlings comes primarily from the soil and from water.

4. Seed-boxes and pots may carry on the infection from one season to the next.

5. High temperature and careless watering are frequently responsible for the rapid spread of the disease. By sowing no thicker than fifty seeds to the box, carefully regulating the watering, picking out diseased seedlings, reducing the temperature as much as possible, and giving sufficient ventilation, the disease may be reduced to a minimum.

6. Soil sterilisation by heat or by formaldehyde completely frees the soil from the disease organisms, and thus, provided the water is non-infective, gives protection. In order to ensure a healthy crop of seedlings, all seeds should therefore be sown and "potted up" in sterilised soil.

7. The application of a fine mixture of 10 parts of dry slaked lime and 1 part of copper sulphate at the rate of $\frac{3}{4}$ oz. to the square foot is useful in reducing the amount of the disease.

ON THE OCCURRENCE IN BRITAIN OF THE CONIDIAL STAGE OF *SCLEROTINIA MESPILI* SCHELL

By H. WORMALD.

(*South-Eastern Agricultural College, Wye, Kent.*)

(With Plate XI and 2 Text-figures.)

WHILE engaged in an investigation of the Brown Rot diseases of fruit trees in this country the writer was informed that for a number of years medlar trees (*Mespilus germanica* L.) in a cherry orchard near Sittingbourne, Kent, had suffered from a disease supposed to be a form of Brown Rot. The grower was asked to send specimens to Wye College in the event of the reappearance of the disease and in the middle of April of the present year (1920) medlar shoots were received, the leaves of which showed dark-brown blotches varying in size from about 1 cm. in diameter upwards; in a few cases the whole leaf was affected and completely withered. No organism was visible on the surface of the leaves when received but, on placing the specimens in a moist chamber, grey tufts appeared on the upper surface of one of the dead leaves within four days. Microscopic examination showed the tufts to consist of chains of rather large spherical conidia; many of the conidia floated free when placed in a drop of water but others were seen to be connected by slender fusoid bodies and it was at once realised that the fungus was the conidial stage of one of the Sclerotinias of the *S. Linhartiana* type, *i.e.* those in which the conidia become separated by "disjunctors." This term was introduced by Woronin[1] who found and described the development of these bodies in *Sclerotinia Vaccinii*.

The diseased leaves emitted a strong sweetish odour which was particularly noticeable on opening the glass case in which such leaves had been confined for two or three days. Healthy leaves kept under similar conditions did not give off this characteristic odour.

No record could be found of the occurrence of this disease in Britain[2], but reference to Continental mycological literature showed that a similar disease and fungus had been recorded for Switzerland and described in an interesting paper by Schellenberg[1] in 1907. He had observed the diseased condition of the leaves in the open in 1905 and induced the development of the conidial fructifications on diseased leaves which he had collected; in the following year he found the apothecial form, which he named *Sclerotinia Mespili*, on mummified medlar fruit and described the mode of infection of medlar leaves by the ascospores. Schellenberg remarked on the peculiar odour given off from diseased leaves and stated that it attracts insects which carry the conidia (the "chlamydospores" of Schellenberg) to the medlar flowers and so cause infection of the latter. He attributed the odour to the conidial fructifications ("so zeigen diese Chlamydosporenrasen einen ausgesprochenen, starken Duft[2]"), but the present writer found that diseased leaves on which conidia had not yet appeared were decidedly odoriferous, and a more probable explanation of the phenomenon is that it is caused by an enzymic secretion of the fungus acting on one or more organic compounds present in the tissues of the leaves.

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[1] Woronin, M. "Die Sklerotienkrankheit der Vaccinienbeere," *Mém. de l'Acad. de St Pétersbourg*, Série 7, T. XXXVI, 1880.

[2] The author is indebted to Miss E. M. Wakefield and Mr J. Ramsbottom for their aid in consulting literature at the Kew Herbarium and at the Natural History Museum respectively.

A few days after the specimens were received a visit was paid to the orchard with the object of ascertaining the source of infection, particularly as Schellenberg's work suggested that the spring infection of the leaves is caused by ascospores discharged from apothecia which develop from mummified fruit lying on the ground. The diseased trees were three in number and on each of them about 25 per cent of the flowering shoots were affected, from one to three leaves on each shoot showing the characteristic blotches (Fig. 1); in some cases two distinct spots were found on the same leaf. No conidial fructifications could be found on the leaves on this occasion so that it would appear that the brown areas represented primary infections, and although there must have been some hundreds of such primary infection spots on each tree, the source of infection was not discovered. Numerous undeveloped mummified fruits had remained on the trees from the previous year, but no conidial fructifications, corresponding to those which later developed on the leaves, could be found on them. Similar mummified fruits were found on the ground, but, although a careful search was made no apothecia were discovered.

Towards the end of the same month (April), medlar shoots with leaves similarly affected were sent in from Faversham; on some of these shoots as many as four leaves were infected and, in a few cases, the discoloration had extended from the laminae along the petioles and into the axes of the shoots. During May further specimens showing the same disease were obtained from Maidstone, Margate, and Weston-super-Mare (Somerset)[1]. The diseased trees at Faversham and Maidstone (one large tree in each case) were examined by the writer early in May; by this time conidial fructifications were to be seen on some of the diseased leaves in the open. These fructifications were again confined to the upper surface of the leaves and were sometimes in the form of small, scattered, grey tufts, but usually these soon became confluent to form continuous patches or strips which generally followed the lines of the midrib and chief veins (Plate XI, fig. 2).

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[1] Schellenberg, H. C. "Ueber Sclerotinia Mespili und Sclerotinia Ariae," *Cent. für Bakt.* Abt. 2, Bd XVII, 188–202, 1907.

[2] *L.c.*, p. 193.

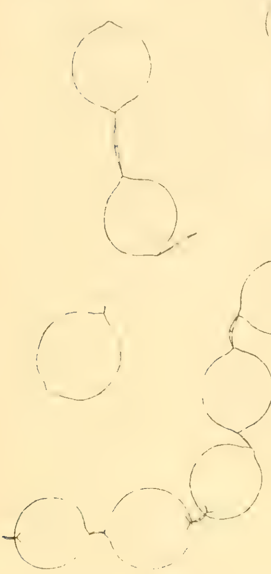

Fig. 1.

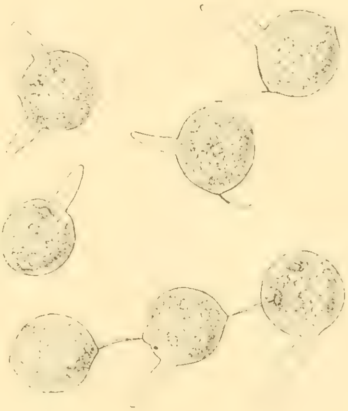

Fig. 2.

Fig. 1. Conidia and disjunctors (× 500).

Fig. 2. Conidia germinating in distilled water (× 500).

The conidia were approximately isodiametric; the longitudinal axis was generally a little longer than the transverse because of the polar papillae, which were from 0·5 to 2μ in length, usually about 1μ. Conidia produced on a leaf in the open were measured and found to be from 12 × 10·5μ to 25 × 20·5μ (mostly 18–22 × 16–20μ), with an average (of 100 conidia) of 19·3 × 17·1μ; these dimensions are in close conformity with those given by Schellenberg which are 15–18–20μ.

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[1] Mr W. F. Emptage kindly supplied me with specimens from Weston-super-Mare.

The disjunctors were from 3–11μ, or more, in length (usually 6–9μ); one conidium was attached to its neighbours by disjunctors 14 and 15μ long respectively, and one disjunctor as long as 17μ was observed, but such instances were exceptional. Schellenberg writes, "Der Disjunktor zwischen den einzelnen Sporen wird kräftig ausgebildet und misst 1·5–2μ"; his illustration of a conidial chain however shows disjunctors 3–5·5μ in length.

Some of the mummified fruits (or rather flowers, since they had remained practically undeveloped) were collected from the trees and examined microscopically; mycelium was found within the tissues, and agar cultures obtained from such mycelium resembled those produced from conidia. Particles of the superficial layers of these mummified flowers, when teased out in water, yielded numerous minute (about 3μ in diameter), spherical, spore-like bodies which are probably the "microconidia" described by Schellenberg. Similar microconidia or "sporidia" are produced by the fungus in agar cultures. In size and mode of development they resemble the microconidia produced by *Sclerotinia cinerea* and *S. fructigena* when these are cultivated under laboratory conditions, and also in the fact that they are not known to germinate.

The macroconidia however germinated readily in distilled water and germ tubes about 20μ long were produced within four hours, some of the germinating conidia being still attached to one another by the disjunctors (Text-fig. 2). They also germinated on prune juice agar and on agar prepared with a decoction of medlar leaves, but growth was very slow as compared with that of *Sclerotinia fructigena* or *S. cinerea* when growing on agar culture media. These cultures of *S. Mespili* produced pustules of microconidia but no macroconidia. On agar containing an extract of medlar leaves the cultures were dark brown and the browning extended into the culture medium in advance of the hyphae.

The apparent strict specialisation of the fungus is a feature of practical interest. Two of the outbreaks occurred on medlar trees growing in cherry orchards and the owners were desirous to know whether the medlar leaves were likely to prove a source of infection for the cherries. *Sclerotinia Mespili* is not known to attack cherry trees, but there is no experimental evidence to show that it is unable to do so. In this connection

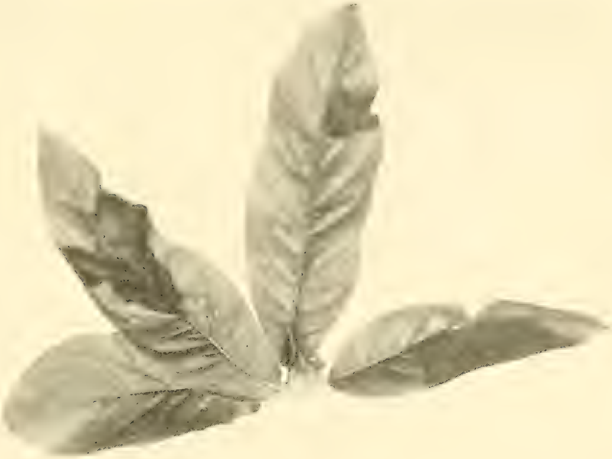

Fig. 1.

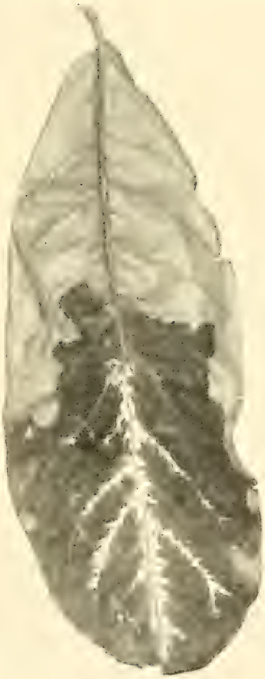

Fig. 2.

Schellenberg writes[1], "Auch die Specialisation des Pilzes ist, wie mir scheint, eine weitgehende, denn der Pilz geht nicht auf die nahe verwandte Quitte über und wie es scheint auch nicht auf *Crataegus*, *Pirus malus* und *communis* und *Prunus Padus*, *avium* und *cerasus*."

On the other hand the writer found on one of the medlar trees a mummified flower bearing three pustules of *Monilia cinerea* and also a leaf with numerous pustules of the same fungus; the medlar therefore under certain conditions may serve as a host for *Sclerotinia cinerea* and so become a source of infection for neighbouring plum and cherry trees.

SUMMARY.

This article records the occurrence, in the spring of 1920, of the conidial form of *Sclerotinia Mespili* Schell. on the leaves of medlar trees in four localities in Kent and one in Somersetshire.

Mycelium obtained from dead flowers which had remained on the tree from the previous year gave rise to cultures similar to those obtained from conidia taken from infected leaves but the *Sclerotinia* stage of the fungus was not observed.

DESCRIPTION OF PLATE XI

Fig. 1. A young flowering shoot of medlar showing three infected leaves ($\times\frac{1}{2}$).

Fig. 2. A diseased medlar leaf showing the conidial fructifications extending along the mid-rib and chief veins of the infected portion ($\times\frac{2}{3}$).

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[1] *L.c.* p. 195.

FRIT FLY (*OSCINIS FRIT*) IN RELATION TO BLINDNESS IN OATS

By A. ROEBUCK.

(*Lecturer in Agricultural Biology, Harper Adams Agricultural College, Newport, Salop.*)

(With Plate XII.)

INTRODUCTION.

THE West Midlands, in common with many other areas in the country, suffers severely from the terrible scourge Frit Fly, and every year apparently one can find fields of oats ruined by its depredations.

During extensive observations on frit flies and oat crops since 1913, I have often noticed a considerable number of "blind" spikelets in the panicles on infested fields.

The continued association of these "blind" spikelets on attacked crops, whereas good crops with little or no trace of the fly show no signs of them, naturally suggests some connection, direct or indirect, with *Oscinis frit* itself.

The suggestion that the spring attack on the tillers so weakened the plant as to render it incapable of nourishing all the flowers produced is scarcely tenable. A comparison of oats with other members of the Graminaceae would almost indicate that weakness in the plant would show itself more particularly in the bottom or top spikelets, the middle ones being usually well nourished, but "blindness" is found anywhere on the panicle.

Similarly in cases of severe grain attack to consider "blindness" due to an early larva destroying the flower as soon as produced and finding insufficient nourishment moving off to other flowers, is unconvincing. The "blind" spikelets are already produced when the panicle unfurls and therefore before the eggs can have been laid in the ears. Moreover, careful examination of the behaviour of larvae in the grain attack has not shown one case where the flowering glumes and palea are destroyed.

The larvae migrate in the spikelets as the food is exhausted and attack very young flowers but the glumes and palea are left.

The only insects I have found in or around these "blind" spikelets have always been those which were apparently sheltering, or possibly attracted in the early season by these white patches in an otherwise uniform green background.

Continuing observations on this problem the following facts were obtained during the summer of 1919 which point to a direct connection between the "blindness" and frit fly.

Observations.

The Blindness, Deafness or White Ear referred to is most noticeable comparatively early in the season when the oat panicles are unfurling from the sheath and are a good deep green colour. The "blind" spikelets then stand out clearly almost white. They consist almost always of the two flowerless glumes, often with branches of the rachis twisted and blanched.

In a field of Abundance oats very severely attacked by frit fly the panicles began to unfurl about the 20th June and large numbers of "blind" spikelets were noticed.

Examination of several ears still enclosed in the swollen sheath on June 24th, revealed the presence of a larva of frit fly in a number of these, feeding amongst the folded flowers. Subsequent examination of unfurled panicles made frequently until the end of July showed in many cases two or even three larvae. The intensity of the attack causing irregular ripening through the production of more tillers, coupled with the fact that plots were sown at different dates extending into May, enabled the observations to be made over this extended period. The larvae were found anywhere amongst the curled up mass of the panicle protected from the outside by the enclosing leaf and destroying completely the enclosed flowers, leaving the blanched flowerless glumes and curled branches of the rachis. In the worst cases the whole panicles were destroyed leaving only the central axis and branches which presented a blanched and twisted appearance on unfurling.

Further search on the same day, June 24th, in those cases where the first spikelets of a panicle had emerged, revealed several pupae. The pupa is fixed amongst the curled up mass, apparently anywhere—on the outside of the spikelet, rarely inside it, on the rachis or more rarely on the inside of the leaf sheathing the panicle.

It is apparently loosely attached though undoubtedly as securely as in the stem or grain attacks. When the panicle pushes out of the enclosing leaf and still more as the panicle itself expands, the pupa is almost invariably forced off and falls to the ground. Many pupae were obtained during the season still attached to the open panicles, but the proportion was very small, so that had the attack been mild or only moderately severe, it would have been very difficult to have found any at all.

An examination of the field therefore seldom gives any indication of the cause of the trouble.

Whether the imagines emerge from pupae on the ground or at the time the ears are unfurling cannot be answered definitely at present, but from the dates of hatching of those obtained one would almost conclude from the ground.

The first fly was hatched indoors on July 2nd, but the main bulk appeared later, approximately the third week in July. This period it must be understood is based on the year's observations only, and most of the specimens were gathered on an area where the dates of sowing varied from March 28th to May 13th giving therefore almost as wide a range of maturing of the crop as it is possible to get.

VARIETIES OF OATS.

The data given above were obtained on a field of Abundance oats, but examination of oat fields over many farms on a wide area fully supported them. A careful study was made of a number of oat varieties, sown on the same day (April 9th), and grown side by side, to see if variety had any effect on the intensity of the "blindness" attack.

The results are given in the table below.

Variety of oats	Percentage of ears containing "blind" spikelets	Variety of oats	Percentage of ears containing "blind" spikelets
Abundance ...	26	Golden Rain ...	58
Thousand Dollar	38	Yielder	56
Banner	47	Dunns	33
Victory	52	Welsh Grey ...	25
Supreme ...	22	Clemrothery ...	49
Record	31	Hero	20
Sandy	26	Crown	44
Potato	74	Blainslee ...	22
Leader	35	Tartar King ...	40
Black Tartarian	30	White Tartar ...	27
White Tartarian	21		

From this it will be seen that all varieties were attacked. It must be remembered that this table deals with ears only, the individual "blind" spikelets were not counted. Hence the table is no criterion of the actual damage, one variety may have had a few ears attacked severely and another a large number of ears attacked slightly.

POSITION OF THIS ATTACK IN THE LIFE CYCLE OF THE FRIT FLY.

In this country entomologists have long recognised three broods—one on grasses, one on the oat stems and another in the oat grains. There has always been a difficulty, if the broods were sharply defined, of the long interval between the tillers dying in spring and the grain being attacked. This difficulty was emphasised by Ritzema Bos as early as 1891. A brood intermediate between the one on the oat stems and the one in the grains has been somewhat uncertain in this country. The association of the name brood with the nature of attack has possibly added somewhat to the uncertainty, but more particularly the apparent overlapping of the broods is a difficulty.

The following table indicates the position of this attack in the life cycle. It is based on field observations in Shropshire extending over five years, except this particular attack, which is on one year.

Site of pupa	Earliest gathered pupa	Period of maximum emergence of flies
Grass stems (Arrhenatherum)	March 25th	1st week of May
Base of oat tillers	May 21st	Middle of June
Panicle inside leaf	June 24th	3rd week of July
Oat grains	July 31st	1st week of September

The period of maximum emergence is given because both stem attack and this attack causing "blindness" continue until harvest as more tillers are produced and more panicles unfurl.

This table would seem to supply evidence in the field in this country in support of dates obtained from indoor cultures by Dobrovliansky in Russia during 1915 (*vide* Collin in *Annals of Applied Biology*, vol. v, p. 85).

CONCLUSION.

From the abundance of evidence obtained last summer I feel justified in suggesting that there may be three broods of frit flies on the oat crop and that "blindness" is caused by the intermediate one. Probably only a certain percentage of the intermediate brood cause this "blindness" —the remainder entering newly forming tillers. Perhaps the scarcity of suitable tillers, in view of the more advanced condition of the crop and the consequent lessening of the light at the base, compels a certain number to choose the next most suitable site, with the results shown.

Exact information on this matter, however, is not available.

Another site for this brood found in some abundance during 1917 was on the stems of winter wheat. The larvae were feeding on the stems from the base to at least the third node up and the pupae were found in the leaf sheath anywhere between the node and the ligule.

DESCRIPTION OF PLATE XII

Fig. 1. Two oat ears attacked with pupae *in situ.* Higher oat ear with pupa on rachis. Lower one with one pupa in centre and one at the base.

Fig. 2. Specimens of frit fly damage on panicles. (The one in the bottom right-hand corner has lost all spikelets.)

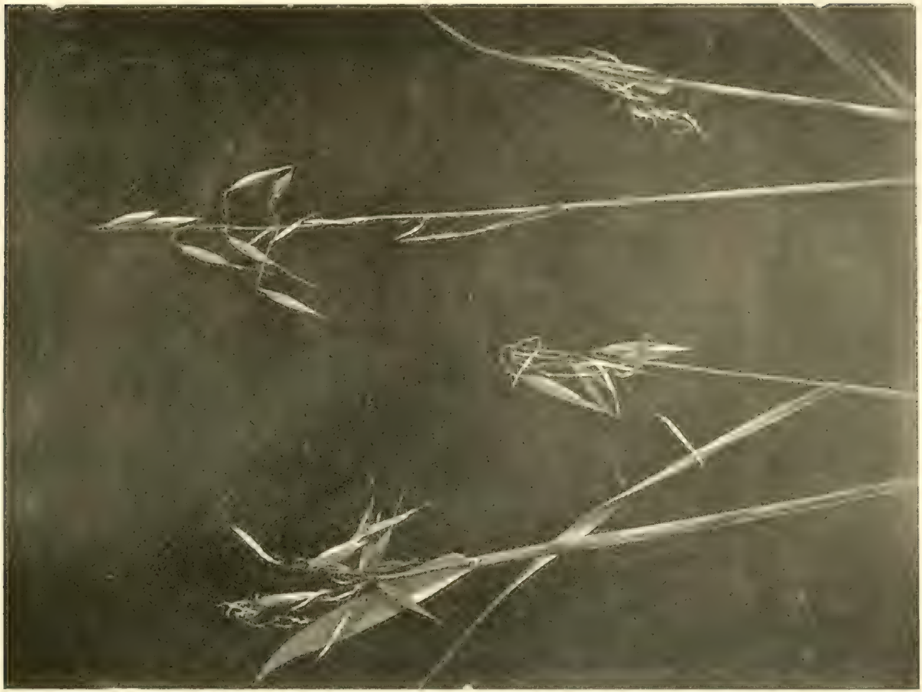

Fig. 2.

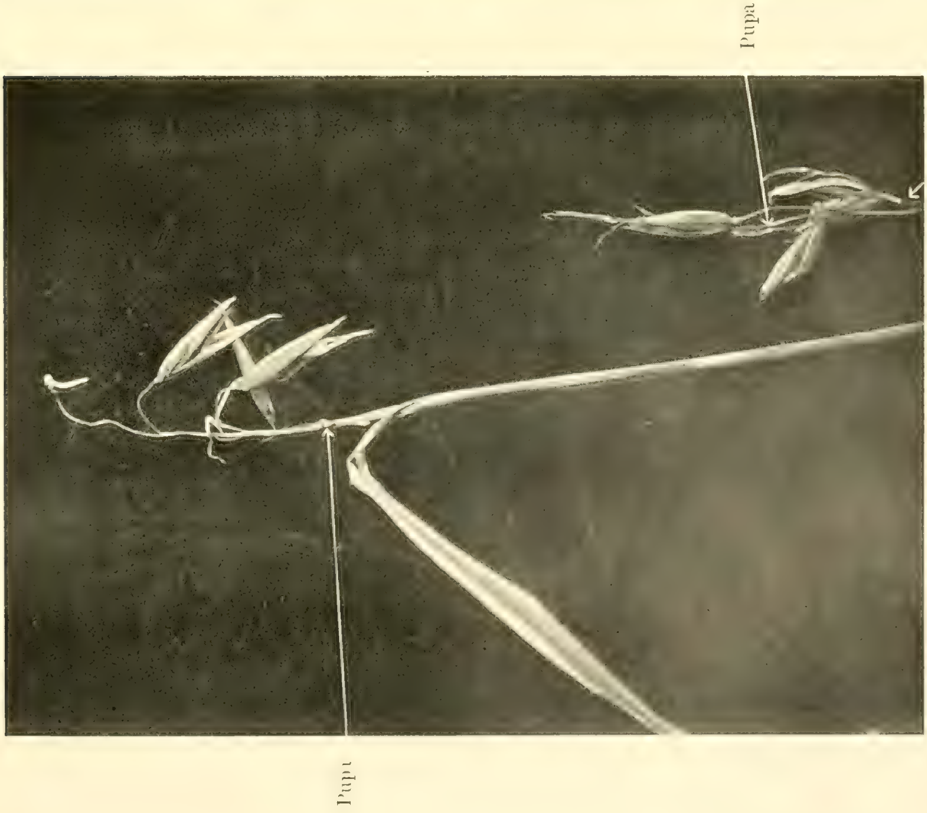
Pupa
Pupa
Pupa

Fig. 1.

MYCOLOGICAL STUDIES. I

ON THE "SPOTTING" OF APPLES IN GREAT BRITAIN

By ARTHUR S. HORNE

AND

ELEANOR VIOLET HORNE.

(*From the Department of Plant Physiology and Pathology, Imperial College of Science and Technology.*)

(With 6 Text-figures.)

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1. INTRODUCTION.

THIS investigation was undertaken with a view to enquiring into the nature and origin of the spots which occur on the surface of a large number of varieties of apple, including many much prized for culinary and dessert purposes in this country; these spots, which begin to appear towards the end of the summer, spoil the appearance of the apple and are often the cause of premature decay.

This "spotting" of apples is prevalent in the United States and investigations have been undertaken or are in progress at several of the Agricultural Experimental Stations there. The earlier workers, notably L. R. Jones (Vermont)[1], Longyear (Michigan)[2] and Lamson (New Hampshire)[3], attributed the "spotting" to various fungi, for example,

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[1] Jones, L. R. *Vt. Agr. Exp. Sta. Rept.* 5 (1891), p. 133.

[2] Longyear, B. O. *Spec. Bull. Mich. Agr. Expt. Sta.* 25 (March, 1904).

[3] Lamson, W. H. *N. H. Coll. Bulls.* Nos. 27 (Apr. 1895), 45 (May, 1897), 65 (May, 1899), 101 (Apr. 1903).

Dothidea pomigena (L. R. Jones), *Phyllachora pomigena* (Schw.) Sacc. (Longyear), but lacked the opportunity to verify their suppositions by cultural experiments.

In 1908 Charles E. Brooks[1] proved by cultural methods that *Cylindrosporium pomi*, in a later paper[2] identified as *Phoma pomi*, was capable of causing "spotting" in the Baldwin variety.

In 1911 W. M. Scott[3] isolated *Cylindrosporium pomi* and species of *Alternaria* from the Jonathan variety, but concludes that the cause of the disease is unknown. *Alternaria* has been obtained also by M. T. Cook and G. W. Martin (1914)[4] from large light brown spots on Jonathan apples.

Finally E. C. Stakman and R. C. Rose[5] have announced an investigation into a fruit spot of the Wealthy apple.

Besides the fungi found during enquiries more directly concerned with the "spotting" of apples, others which generally cause rotting or twig canker have been recorded as causing "spotting," for example, *Phoma mali* Schultz. et Sacc. (Charles E. Lewis[6]), *Physalospora cydonieae* (Clinton)[7], *Phyllosticta solitaria* (John W. Roberts[8]), and *Glomerella cingulata* (Dastur[9]).

In Britain, on the other hand, little work has been done. Towards the end of 1914, some correspondence was published in the *Gardeners' Chronicle*[10] with reference to a disease of apples which was puzzling fruit growers. The apples were covered with sunken spots which often developed after the fruit was stored. The varieties affected at the time were Ecklinville Seedling, Warner's King, Cox's Pomona, James Grieve, and Rival. The disease was also developing in Peasgood's Nonsuch, Gascoigne's Scarlet Seedling, Newton Wonder, and Blenheim Pippin. Fruits of Gascoigne's Seedling remarkable for size and colour, and apparently sound early in November (1914), were at the end of the month unrecognisable through the disease. This disease was thought to be due to *Cylindrosporium pomi*; but it was pointed out that no

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[1] Brooks, Charles E. *Bull. Torr. Bot. Club*, 35 (1908), p. 423.

[2] Brooks, Charles E. and Black, Caroline. *Phyt.* II (1912), p. 63.

[3] Scott, W. M. *Phyt.* I (1911), p. 32.

[4] Cook, M. T. and Martin, G. W. *Phyt.* III (1913), p. 119.

[5] Stakman, E. C. and Rose, R. C. *Phyt.* IV (1914), p. 333.

[6] Lewis, Charles E. *Maine Agr. Exp. Sta. Bull.* No. 170 (1909).

[7] Clinton, G. P. *Connec. Agr. Exp. Sta. Rept.* Part V (1905), p. 264.

[8] Roberts, John W. *U.S.A. Dept. Agr. Bur. Pl. Ind. Bull.* 534 (1917), p. 1.

[9] Dastur, J. F. *Ann. App. Biol.* VI (1920), p. 262.

[10] "A Southern Grower." *Gard. Chron.* No. 1457 (Nov. 28, 1914), p. 357; Cornish, P. E., *l.c.* p. 357.

English mycologist appeared to have given any considerable attention to the subject, and that it was very important that mycologists in this country should be able to inform growers to which malady, whether bitter pit or Cylindrosporium spot, any attack was due.

These considerations furnished the incentive to study the "spotting" problem. Early in the following year we received reports from Kent, Surrey and Berkshire of "spotting" in other varieties, notably in Bramley's Seedling, Cox's Orange Pippin and Allington Pippin, and specimens were forwarded for examination by several fruit growers. It was reported from Kent that very many of the finest and best ripened apples had become covered with very small red spots: this had not prevented the apples from keeping, but it had greatly injured their sale. The trouble developed entirely in apples in store. Barker[1] reported "spotting" in Allington Pippin and Bramley's Seedling from Worcestershire, Cambridgeshire, Oxfordshire and Sussex, and concluded that the trouble was general throughout apple growing districts.

2. SYMPTOMS.

The spots show considerable variety in form and colour. They are sometimes green, of a darker shade than the normal skin colour, as for example in Lord Derby, Newton Wonder, and Reinette du Canada, where dark green blotches show up conspicuously on a yellow-green skin. In the case of a pigmented apple, the spots are usually of a darker shade of red or purple than the normal (Scarlet Nonpareil). In varieties with partial pigmentation, the spots are frequently coloured rose, red or purple (Mrs Philimore, purple spots on a green ground); coloured spots also appear in normally unpigmented varieties such as Old Nonpareil, Reinette du Canada (blotches with purple edging), and Lane's Prince Albert (dark brown blotches bordered pinkish red).

Curiously mottled blotches are sometimes formed with the mottlings in purple, purplish brown and green; for example, Ribston Pippin, Old Nonpareil, Cox's Orange Pippin, Charles Ross (brown, and purplish brown).

Dark brown spots occur in Ecklinville Seedling, Yorkshire Greening, etc.; pale brown spots in Cox's Orange Pippin, Charles Ross, Emperor Alexander, Peasgood's Nonsuch (spots with irregular contour), and Duke of Devonshire. In Hollandbury the spots are dark, of irregular outline, angular and so numerous as to give the apple a fantastic appearance. The dark brown, slightly sunken spots in Wellington resemble a scurf; in Tamplin they are often round, sunken, numerous and very small.

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[1] Barker, B. T. P. *Ann. Rept. Agr. and Hort. Res. Sta., Long Ashton* (1914), pp. 97–99.

Minute black markings of various kinds are frequently present in the brown spots which add a great variety of minute detail. The spot may be almost uniformly black (September Beauty, Rev. W. Wilks, Early River, Wolf River), or black dendritic markings may appear (Newton Wonder). These appearances are due to the presence of fungi with dusky mycelium, for example, *Alternaria*, *Dematium pullulans*, etc. Again, the spot may be dotted in various patterns with the dark sclerotial or other reproductive bodies of various fungi, and the pattern will vary with the kind and degree of development each has attained. The following fungi have been found to produce this "dotted" effect:

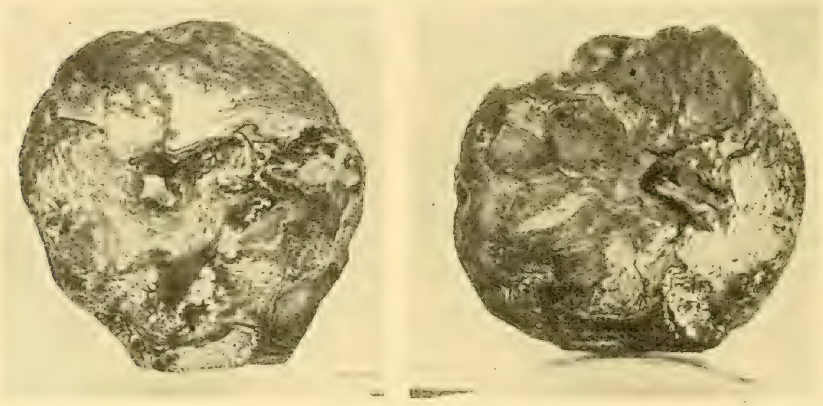
(*a*) (*b*)

Fig. 1. Photographic reproduction showing mummification following "spotting" of apples.

(1) *Pleospora pomorum*—black sterile perithecia.
(2) *Valsa* sp.—necks of the perithecia.
(3) *Polyopeus purpureus*—dark brown pycnidia (Early River, Stirling Castle).
(4) *Myxosporium mali*—black sclerotial bodies.
(5) An unidentified fungus with thick glistening walls—black sclerotia.

Perithecia often escape recognition since only a portion of the perithecium (*Pleospora*), or only the extremity of the neck (*Valsa*) protrudes above the surface of the apple.

It is not meant to be understood that the spots named are necessarily of different origin; a purple spot and a brown may differ in aspect merely through varietal characteristics of the apples on which they occur: conversely, spots of a somewhat similar category—brown spots, for example—should not be held to indicate a likeness of origin, since a brown colour is one of the commonest symptoms of a pathological condition.

Spots of different kinds may occur on the same variety and even on the same apple. There were on Lane's Prince Albert, received from Berkshire at the end of April, 1915, pale brown spots with a dark brown centre; chocolate brown spots with a pale centre, and blackish spots mottled with green; some spots were variously dotted, others not. On other apples of this variety received at the same time, dendritic markings were present on a pale brown ground, and in the same variety greenish and purplish sunken blotches and dark brown spots with a pinkish red border also occur.

"Spotting" has been observed in about one hundred varieties of apple, and occurs in a widely representative series of varieties—early, mid-season and late, and whether culinary, dessert or exhibition—including a number of sorts most prized in commerce. The varieties which escape include hard-fleshed apples, notably the russets (Christmas Pearmain, Worcester Pearmain, etc., with the exception of Hubbard's Pearmain): the late pippins (Allen's Everlasting—a seedling from Sturmer Pippin, Fearn's Pippin, etc.); also, as far as observations of 1917–18 show, certain other varieties with crisp sub-acid flesh, such as Barnack Beauty, Gloria Mundi, Belle Dubois.

"*Spotting*" *in relation to the lenticels.*

The surface of the apple is studded with numerous minute pale, more or less stellate, apertures which are more conspicuous on some varieties than others. These are usually referred to as lenticels[1], although they do not possess the typical structure of such organs. McAlpine[2] states that they are formed through rupture of the stomata as a result of expansion as the apple increases in girth; he gives a photographic reproduction of a pore showing the remains of a stoma (McAlpine, Plate XIV, fig. 102). They take their origin therefore in the same way as lenticels.

In a number of cases the spots originate at the lenticels. A careful examination will show a complete series of stages from discoloured lenticels to spots. In Wellington the smallest spots just encircle the lenticel, and there are others of every intermediate stage between these and the largest in the apple. In Ecklinville Seedling nearly every lenticel in the apple is brown and in a large number of them brownness has spread round to form a spot varying from the size of the lenticel itself to one-eighth of an inch in diameter. On Stirling Castle with dark spots the lenticels show up conspicuously brown. On Golden Spire there are dark brown spots on one apple and pale brown on another, the size of a pin's head. On Lane's Prince Albert received in December 1915 from Berkshire, the smallest spots were of the same dimension as the lenticels.

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[1] The stomata are not all ruptured by the time the apple reaches maturity: stomata were observed quite late in the season in a large specimen of an unknown variety.

[2] McAlpine. "Bitter Pit Investigation," *First Progress Report* (1911–12), p. 40.

These observations confirm those of Charles Brooks[1], Barker[2], Cook and Martin[3] and others as to the importance of the lenticel in relation to incipient "spotting"; but the lenticels are not the only centres of origin, since the opportunity for infection occurs wherever stomata exist or where the skin is injured by cracks or wounds of any kind.

Development of "spotting."

"Spotting" usually appears towards the end of July, and there is a considerable development in August. On September 29th, 1915, "spotting" was observed on 31 varieties at Wisley. The production of new spots goes on continuously throughout the storage period until the coming of spring: over 200 spots were counted on a specimen received from Sussex in 1915.

The progress of "spotting" was specially studied in a collection of over ninety varieties of apples at the Royal Horticultural Society's Gardens in 1917–18, from two to four specimens of each variety being examined. Of these, 30 varieties remained free during the season. In some kinds spots developed early in the season and remained without further development; for example, in King of Tomkins County (seasonal period September–April), depressed blackish brown spots up to $\frac{1}{4}$ in. diameter were present early in November, but remained with little increase in size until May. In others, there was a steady increase in size; thus in Ribston Pippin (November–January) numerous minute brown spots were present early in November: these increased to $\frac{1}{8}$ in. (November 22nd) and $\frac{1}{4}$ in. in diameter (November 28th); soon afterwards the apples became rotten. In Yorkshire Greening (October–January), there were few depressed brown spots and brown spots with a black centre up to ¼ in. in diameter; these remained arrested until January 31st, when the largest spot was 1 in. in diameter; the apple then rotted. In over 20 varieties, rotting which could be traced to "spotting" had set in before the varieties were out of season.

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[1] Brooks, Charles E. *Bull. Torr. Bot. Club.* 35 (1908), p. 423.

[2] Barker, B. T. P. *Ann. Rept. Agr. and Hort. Res. Sta., Long Ashton* (1914), p. 98.

[3] Cooke, M. T. and Martin, G. W. *Phyt. l.c.*

3. THE FUNGI CONCERNED.

Owing to the fact that so few of the black bodies found in "spot" areas proved fertile, cultural methods were adopted in the hope that reproductive bodies which would facilitate the work of identification, would be formed in the media employed.

The apple was first washed in ·1 per cent. mercuric chloride solution, and then rinsed thoroughly in sterile water: small cubes from 1–5 mm. long were cut out rapidly with a sterile knife and dropped into apple extract or on the surface of apple agar—in some cases the cubes were immersed for a few seconds in mercuric chloride followed by washing in sterile water before they were transferred to the medium. Control cubes were taken from unspotted parts of the apple and invariably gave negative results. Cubes taken from bitter pit areas also yielded negative results.

The first fungi were isolated in the autumn of 1915, but owing to circumstances a number of cultures were abandoned and only those considered to be of importance at the time were carried on. Further work was started in the autumn and winter 1917–18 and another series of cultures obtained: these included all the fungi carried on from 1915, with the exception of species of *Alternaria* and *Sclerotium*, and in addition a number of others which were not obtained in the first period.

The total number of isolations in both periods exceeds 400: of these, 140 were in the first period and 260 in the second. The actual number of failures to isolate fungi in the first period exceeded 50 per cent., due in some cases to the use of liquid apple extract, and in others to over-sterilising in mercuric chloride the inoculation cubes. In the second period out of 38 placed in extract, 19 failed—exactly 50 per cent., whereas of those placed on apple agar only seven failed, being cubes obtained from four varieties of apple.

The fungi present in the original cultures were separated by plating out or by transference to slant tubes; in this way several fungi whose identity could be determined were obtained in pure culture; and notably *Leptosphaeria vagabunda* Sacc., *Coryneum foliicolum* Fuck, *Fusarium* *mali*[1] Allersch., *Myxosporium mali*[2] Bresadola and *Alternaria grossularieae* Jacz[3].

Others whose identity could not be determined were regarded as separate fungi from the fact that the general characteristics remained fairly constant in successive sub-cultures. They were transferred to potato mush agar in the autumn of 1918 and in the majority of cases reproductive bodies were formed. These fungi[4] include:

(*a*) Species of a phomoid genus differing from *Phoma* in possessing compound, unilocular pycnidia with multiple necks, to which the name *Polyopeus*[5] is given—*P. purpureus*, *P. pomi*, *P. recurvatus* and *P. aureus*.

(*b*) An aggregate species of *Fuckelia*—*F. botryoidea*.

(*c*) A species of *Coniothyrium* with lobed pycnidia—*C. convolutum*, and a form of *C. cydoniae*.

(*d*) A species of *Alternaria* forming in media "pockets" of conidia —*A. pomicola*.

(*e*) A species of *Pleospora*—*P. pomorum*, with a dematiaceous stage of the *Stemphylium pyriforme* type. The identity of the conidial and ascigerous stages has been proved by reciprocal single spore cultures.

(*f*) A species of *Sclerotium*—*S. stellatum*, somewhat resembling *S. bataticolum*[6].

Three other fungi have not yet formed reproductive bodies rendering identification impossible; they are:

(*a*) The thick-walled fungus to which reference has been made.

(*b*) A slow-growing fungus presenting a dingy white and somewhat powdery appearance at the surface of the medium when grown on apple agar. This fungus was obtained 21 times from spots, with a centrally situated lenticel, varying in size from $\frac{1}{16}$ to $\frac{1}{8}$ in. in diameter.

(*c*) A sterile fungus, isolated from Ben's Red and King of Tomkins County, producing brilliant colours when grown on different media. On apple agar the colours vary from dull pink to bright orange-yellow; on potato slants they vary from pink to yellow, yellow-green with a metallic lustre and orange, and on potato agar plates bright shades of green and blue have appeared.

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[1] See Allescher. *Ber. Bot. Ver. Landshut.* XII, p. 130 (1892); and Oudemans, *Cat. Champ. Pays Bas*, p. 531.

[2] See Bresadola. *Hedwigia*, p. 382 (1897).

[3] This apple Alternaria proved morphologically identical with *Alternaria grossularieae* (Jaczewsky, *Bull. Soc. Myc. Fr.* XXII, 1906, p. 122), isolated by one of us from gooseberries.

[4] For descriptions of the new species see the *Journal of Botany*, vol. LVIII, p. 239. (Oct. 1920).

[5] The morphological and physiological characteristics of this genus will be described elsewhere.

[6] Tubenhaus, J. J. *Phyt.* III (1913), p. 164; also Martin, William H. *Phyt.* VII (1917), p. 308.

The effect produced by these various fungi in the tissues of the apple can only be outlined in very general terms. In sections through a small spot, where of course there may be one fungus or two or more associated fungi, the mycelium is present in the air spaces: the hyphae penetrate between the cells and envelop them in a web of filaments firmly adhering to the cell wall. The cells lose their hyaline character through changes in the protoplasm and plastids, and become brown—the tissue is darker when fungi with dusky mycelium are present. In some cases mycelium is present in a hyaline zone in advance of the discoloured region.

SPECIAL RELATIONS OF THE FUNGI CONCERNED IN "SPOTTING."

The fungi isolated from the smallest spots ($\frac{1}{16}$–$\frac{1}{8}$ in. diam.) include *Pleospora pomorum*[1], *Leptosphaeria vagabunda*, *Polyopeus purpureus*, *P. pomi*, *P. recurvatus*, *P. aureus*, *Fuckelia botryoidea*, *Coniothyrium convolutum*, *Alternaria grossularieae*, *Coryneum foliicolum*, *Myxosporium mali* and certain unidentified forms. Among these fungi are to be sought those responsible for the commencement of "spotting."

In the majority of cases small spots have yielded only one fungus, for example *Alternaria grossularieae* (Ben's Red); *Polyopeus purpureus* (Byford Wonder, Charles Ross, Bismarck). But spots of this category even when occurring on the same apple have not always yielded the same fungus, for example, the brown spots on Margil yielded *Polyopeus aureus*; the dark brown spots, *Fuckelia botryoidea*; again the pale brown spots on Frogmore Prolific yielded *Fuckelia botryoidea*; other spots, *Leptosphaeria vagabunda*. On September Beauty two spots yielded *Alternaria grossularieae* and two *Polyopeus purpureus*. Alternaria and Polyopeus spots occur also on Wolf River and Grenadier.

In some cases two or more fungi may be associated in small spots; for example, *Alternaria grossularieae*, *Polyopeus purpureus* and an unidentified fungus, in Byford Wonder. Here we have two fungi associated which in the same variety also occur singly in spots. In a spot on the variety Rev. Wilks, somewhat larger than those above mentioned, certain spots yield only *Alternaria grossularieae*, but other spots on the same apple yield the same fungus in association with *Myxosporium mali*.

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[1] For the apple varieties from which *Pleospora pomorum* and other fungi have been isolated, see *Journal of Botany*, *l.c.* and *The Gardeners' Chronicle*, vol. LXVIII, October 30, 1920, p. 216.

As regards the frequency with which a particular fungus occurs alone in spots, data can only be given for *Pleospora pomorum* and fungus *b*; the former was found unassociated in eight out of nine varieties studied (in the ninth case *Polyopeus purpureus* was present in addition); in the latter, in 12 out of 15.

Taking into account the total number of spots of all categories, *Pleospora pomorum*[1] has been isolated from 18, *Polyopeus purpureus* from 20 varieties. Only six of these varieties yielded both fungi. *Alternaria grossularieae* occurred in seven varieties of which two (Byford Wonder and Ben's Red) also yielded *Pleospora*, and four (Early River, Grenadier, Rev. W. Wilks, and September Beauty) *Polyopeus purpureus*.

The apples from which *Pleospora pomorum* has been isolated are by no means of a similar class; they include dessert (Cox's Orange, Ben's Red), culinary and dessert (Bramley's Seedling, Wealthy), and culinary (Byford Wonder) sorts; also varieties in season in late autumn (Loddington), and in winter (King of Tomkins County). *Polyopeus purpureus* occurs also in both culinary and dessert varieties, and notably in the culinary varieties Newton Wonder and Lane's Prince Albert, varieties with a wide seasonal range, but it also occurs in varieties with a restricted range as Grenadier.

Fungus *b* has been isolated from dessert and culinary sorts—Alfriston (Nov.–Apl.), Lord Hindlip (Jan.–May), Belle de Pontoise (Dec.–Feb.), Duke of Devonshire (Mar.–Apl.), etc.—chiefly from apples in season after November.

The surface spots present on apples badly affected with "bitter pit" frequently yielded fungi; for example, on Newton Wonder some spots yielded *Cladosporium epiphyllum*, others *Dematium pullulans* and fungus *b*, others slow-growing unidentified fungi (minute dark brown spots). Fungi were not obtained from "spotted" specimens of Calville Boisbunel, Crawley Beauty, Sanspareil and Yorkshire Greening.

The largest spot-flora has been obtained from Cox's Orange Pippin—eight species excluding unnamed fungi: two fungi were obtained from Blenheim Orange, fungus *b* from small spots and later *Myxosporium mali*[2] from areas where rot had set in.

Of the important culinary varieties, Lane's Prince Albert yielded *Dematium pullulans* four times, *Polyopeus purpureus*, *recurvatus*, and

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[1] The earliest date on which it has been obtained is Nov. 15th (Charles Ross), and the latest, early in March (Bismarck).

[2] Also isolated from Byford Wonder, Domino, Duke of Devonshire, Lord Grosvenor, Lord Suffield, Rev. W. Wilks, Winter Hawthornden.

Cephalothecium roseum; Newton Wonder, *Polyopeus purpureus*, fungus *b* four times and *Cladosporium epiphyllum* twice; Potts's Seedling, *Polyopeus. purpureus, Cladosporium epiphyllum, Fusarium mali*, and unidentified fungi; Ecklinville Seedling, *Dematium pullulans*[1] and fungus *b*; Bramley's Seedling, *Pleospora pomorum, Cladosporium epiphyllum*[2] and unidentified fungi; Peasgood's Nonsuch, unidentified fungi (reddish brown spots).

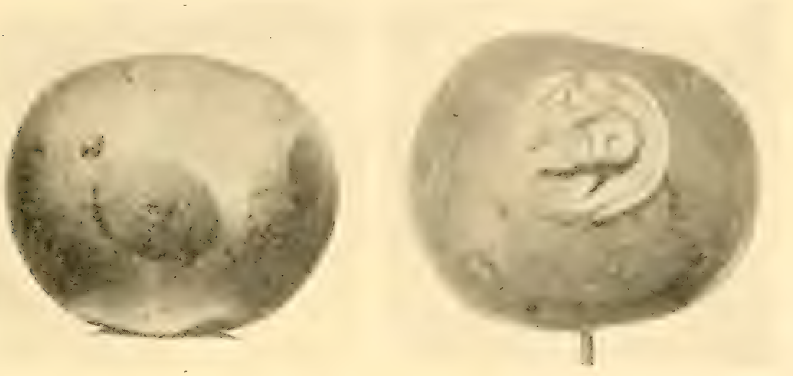
(*a*) (*b*)

Fig. 2 (*a*). Photographic reproduction of an apple inoculated with conidia of *Pleospora* at two points, after seven weeks, showing infertile perithecia (see Fig. 3 *a* for representation of the same apple after two weeks).

(*b*) Photographic representation of an apple inoculated with conidia of *Pleospora* at four points, after seven weeks (see Fig. 3 *d* for a diagrammatic representation of the same apple).

5. INOCULATIONS WITH *PLEOSPORA*[3] *POMORUM* HORNE.

On Jan. 17th, 1917, an apple of unknown variety was inoculated at four points by introducing, through punctures made with a sterile needle, fragments of mycelium bearing conidia (*Stemphylium*) of *Pleospora pomorum*. Five days afterwards, spots were observed at the points of inoculation. On Feb. 22nd, large dark brown areas had developed, and the apple was rotting. Since other spots had formed at points not inoculated another sound apple was inoculated on Jan. 17th, and a number of control punctures were made on a third apple. On Feb. 22nd, brown spots $\frac{1}{4}$ in. diameter were observed, but again spots appeared at places not inoculated. However, on Feb. 28th, the four spots formed at the points of inoculation on this apple had coalesced to form an area 1 in. in diameter. The apple was then cut open and portions of diseased tissue were removed from the interior at a depth of $\frac{1}{2}$ in. from the surface.

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[1] Also isolated from Allington Pippin, Christie Manson, Crawley Beauty, Lord Suffield, Tamplin, Scarlet Nonpariel, Stirling Castle.

[2] Also isolated from small spots in association with other fungi in Christie Manson, Landsburger Reinette, Lord Suffield, Tamplin and Winter Quarrenden.

[3] A full account of the reactions to various media is omitted for reasons of space.

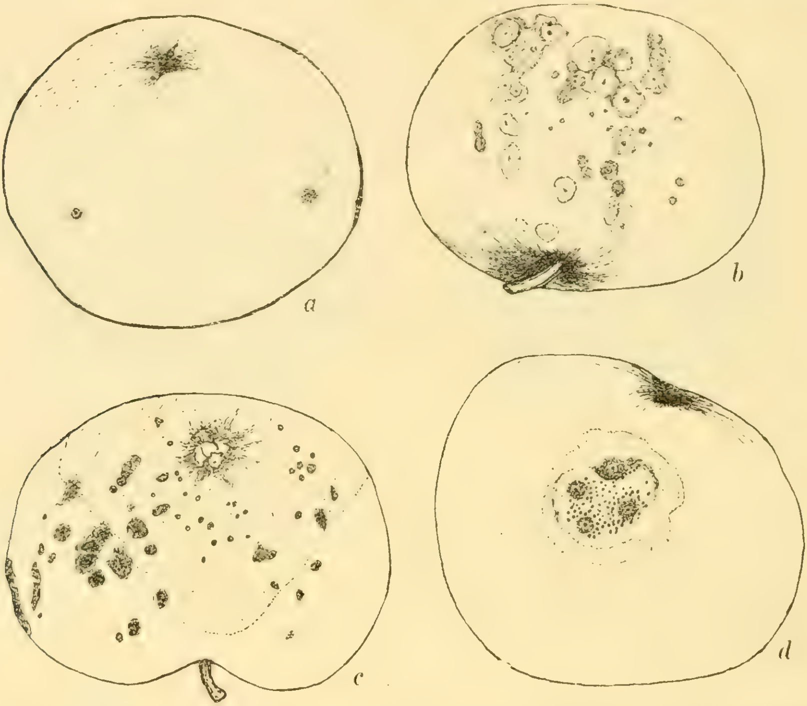

Fig. 3 (*a*). Apple inoculated with conidia of *Pleospora* at two points, after two weeks (see Fig. 2 *a* for photographic reproduction of the same apple after seven weeks).
(*b*) Apple affected with "spotting," March, 1915.
(*c*) Apple showing rot (shaded portion) following "spotting."
(*d*) Apple inoculated with conidia of *Pleospora* at four points, after seven weeks, showing infertile perithecia (see Fig. 2 *b* for a photographic reproduction of the same apple).

Some portions were placed in sterile petri dishes and others on the surface of apple agar in slant tubes. After a few days abundant conidia and later sterile perithecia of *Pleospora* were formed in both dishes and tubes.

Experiments were then made with known varieties. Specimens of Lane's Prince Albert and Newton Wonder were inoculated on March 14th. In the case of Lane's Prince Albert a spot about $\frac{3}{8}$ in. in diameter was present on April 3rd, increasing to a pale brown area with dark centre

1½ ins. in diameter on April 11th and 2¼ ins. in diameter on April 23rd; in the case of Newton Wonder, small spots ⅛ in. in diameter were present on April 11th which increased to ½ in. on April 23rd. In both cases black, sterile perithecia of *Pleospora* developed in the diseased areas.

A number of apples were inoculated with *Pleospora pomorum* while still on the tree in August, 1917. A representative series of varieties was chosen including two varieties, viz. Bismarck and Charles Ross, from which this fungus had been isolated.

The method adopted was as follows: two spot-free apples were chosen of each variety and punctures made (using a sterile needle) in each; one apple was inoculated with a minute fragment of mycelium bearing conidia, and the other not inoculated. After inoculation the apples were enclosed in manilla bags similar to those used in pollination experiments. The apples, by design, were not sterilised before inoculation, as it was desired not to injure the surface of the apple in any way. The inoculant was therefore exposed to competition from fungi already present on the apple. Records of the appearance, etc., were taken at short intervals. As the apples ripened they were removed from the tree and stored under suitable conditions.

Of the 28 varieties inoculated, spots were not formed at the point of inoculation in five, viz. the firm-fleshed russet—Court Pender Platt, Norfolk Beaufin[1], Charles Ross[2], Ribston Pippin and Cellini. Small spots were formed which remained arrested for a period in seven varieties, of which five are culinary sorts—Alfriston, Allen's Everlasting, Beauty of Kent, Calville Boisbunel, Cockle's Pippin, King of the Pippins and Lord Derby. The remaining 16 varieties developed "spotting" more or less rapidly and rotting ensued—Allington Pippin, Belle de Pontoise, Bismarck, Bramley's Seedling, Cardinal, Crawley Beauty, Duchess Favourite, Early Victoria, Grenadier, Keswick Codling, Lane's Prince Albert, Potts's Seedling, Red Astrachan, Rival, Royal Jubilee and Wealthy.

In the case of five of the 16 varieties which eventually rotted—Allington Pippin (Jan 11th), Rival (Jan. 11th), Wealthy (Dec. 31st), Royal Jubilee and Cardinal—*Pleospora was re-isolated from the diseased tissue.* In the first four of these the development of spotting occurred between Sept. 12th and the end of November, that is approximately the time these varieties are in season. In the early variety, Cardinal, rotting took place earlier. A sound Cardinal apple placed in contact with the diseased specimen rotted within a month.

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[1] Large natural spots formed on the inoculated apples.

[2] The failure to infect Charles Ross is noteworthy, since *Pleospora* was isolated from this variety on Oct. 25th, 1915.

In the case of the varieties Rival, Wealthy, and Allington Pippin, *no fungus other than Pleospora was isolated from the rotting areas which developed in the apples inoculated with Pleospora.*

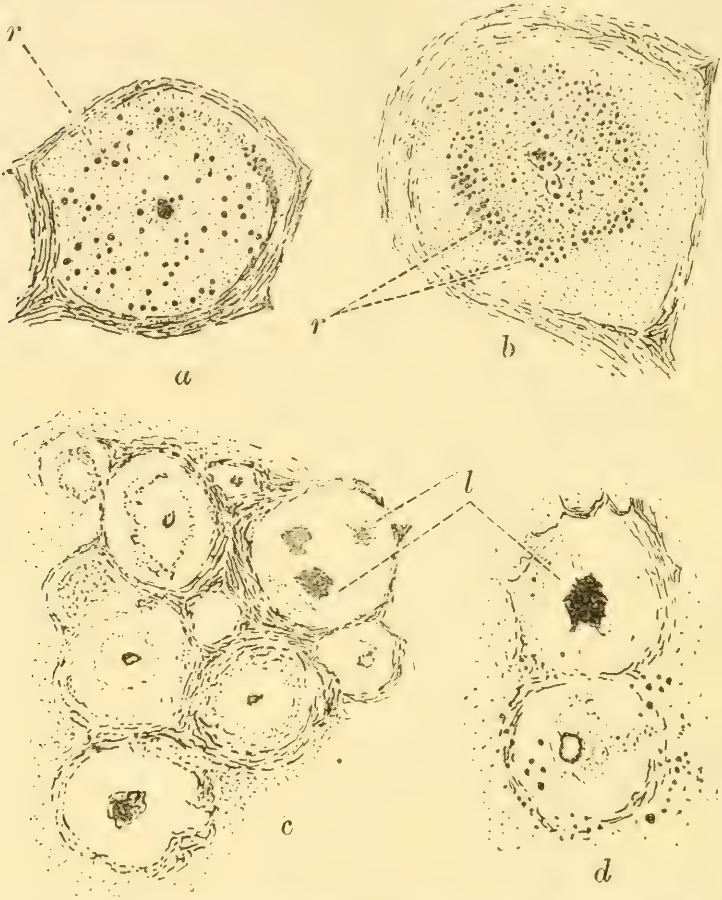

Fig. 4 (*a*–*b*). "Spots" on surface of apple enlarged showing black reproductive bodies of fungi (*r*). (*c*–*d*). Group of "spots" enlarged showing lenticels (*l*).

In the case of the Cardinal apple, however, the presence of a second fungus, *Polyopeus purpureus*, in the diseased tissue was revealed from re-isolation tests made after Sept. 13th. On the following day cubes from the diseased portions in which *Pleospora* mycelium was present were placed in petri dishes in a moist atmosphere. The mycelium which developed was carried on in plate culture and eventually yielded either *Pleospora* or *Polyopeus purpureus*, or both. On Sept. 20th, some more cubes were cut and dropped on the surface of apple agar in slant tubes. On this occasion abundant conidia (*Stemphylium*) were produced within four days, but no *Polyopeus*. On Sept. 26th masses of white mycelium

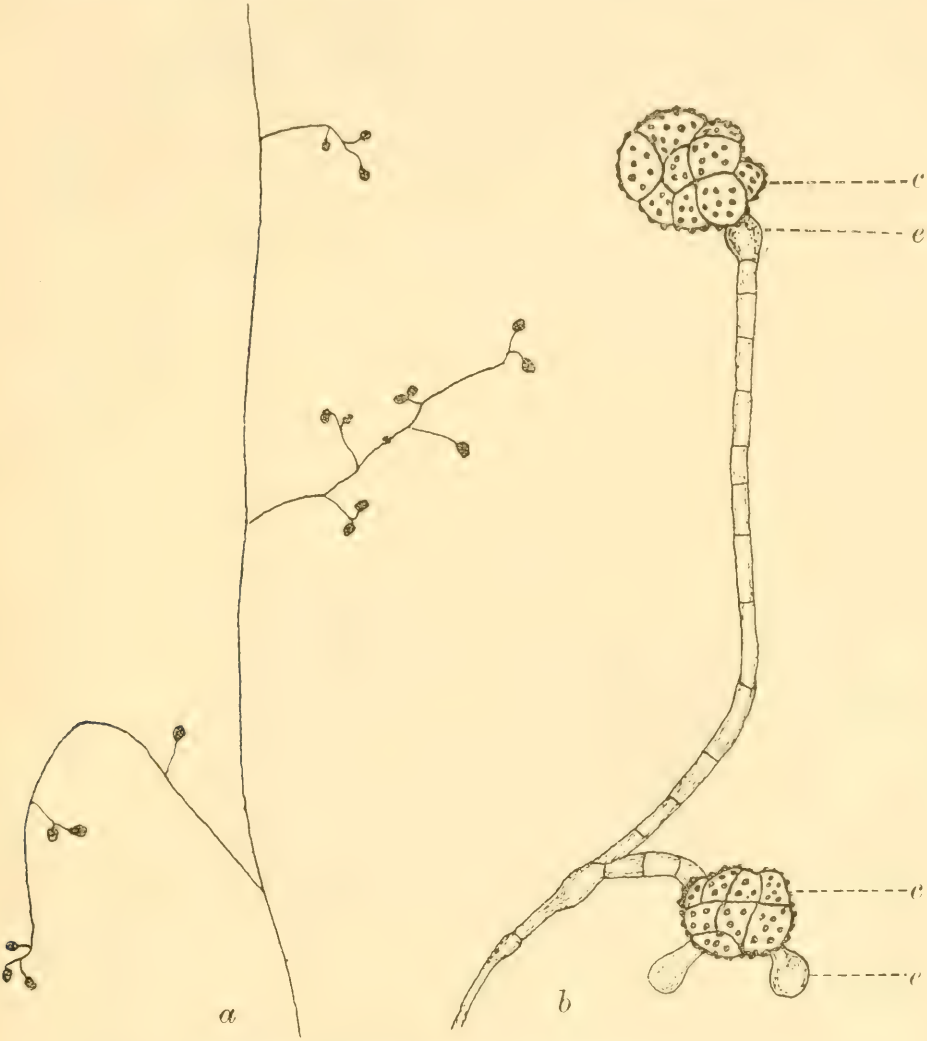

Fig. 5. Conidial stage of *Pleospora pomorum* (*Stemphylium*).
(*a*) Portion of conidiophore.
(*b*) Sporophore showing swollen end-cells (*e*) and mature conidia (*c*).

appeared at the surface of the apple: two tubes of agar were inoculated and yielded on Oct. 2nd, *Pleospora* and *Polyopeus purpureus* respectively.

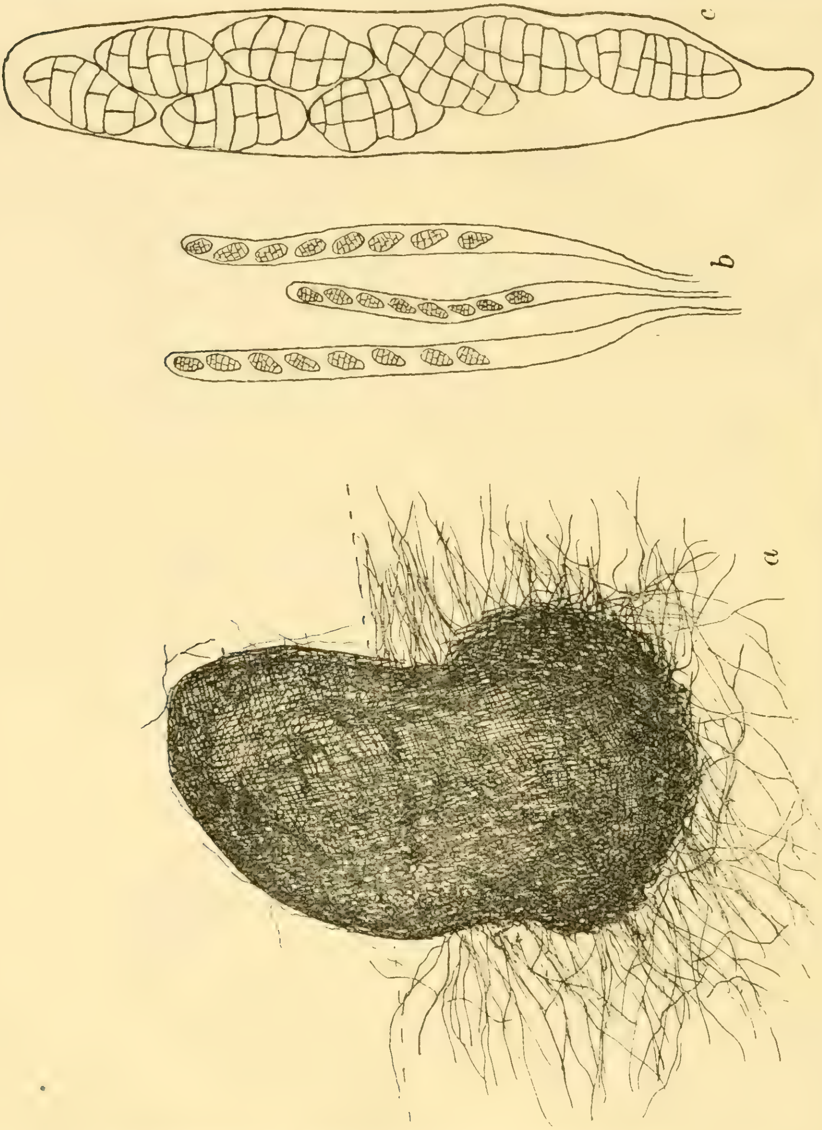

Fig. 6. Ascigerous stage of *Pleospora pomorum*.
(*a*) Perithecium. (*b*) Asci with spores in a single rank. (*c*) Ascus with spores in a double rank.

In Potts's Seedling (Sept.–Oct.), the diseased tissue obtained from artificially produced spots repeatedly yielded *Polyopeus purpureus* and not *Pleospora*. A spot which appeared naturally on the same apple also yielded *Polyopeus purpureus*, but with *Fusarium mali* in addition. Another natural spot yielded an unidentified fungus. In this variety, *Pleospora* has made no progress, but a different fungus, *Polyopeus purpureus*, occurring in the natural spots on the same apple, has effected an entry[1] at the points where *Pleospora* was introduced. Again *Pleospora* was not re-isolated from Lane's Prince Albert, a variety with a wider seasonal range (Oct.–Mar.), but *Polyopeus purpureus* and another phomoid fungus were obtained instead from the artificially produced spots.

The results obtained in Grenadier (Sept.–Oct.) were somewhat different. Small brown spots appeared at the point of inoculation on Sept. 12th. These measured 3 mm. in diameter on Sept. 24th. On this date other spots were forming at the lenticels near the point of inoculation. A month later the original spots formed merely the nucleus of brown areas; in fact the apple was in a semi-rotten condition. On Nov. 8th fragments of tissue removed with sterile instruments from the diseased area near the original point of inoculation were placed on the surface of apple agar in slant tubes. After a few days *Polyopeus purpureus* and *Alternaria grossularieae* were present in the cultures. Cultures made in the same way but using tissue taken 2 ins. from the point of inoculation yielded *Alternaria grossularieae*. Finally, cultures made using eruptive mycelium taken from pustules appearing at the surface of the apple (Oct. 29th) yielded *Polyopeus purpureus*. *Pleospora pomorum* was not obtained at all, but instead two other fungi—*Polyopeus purpureus* and *Alternaria grossularieae*—which were not present in the inoculant.

6. CONTROL.

Susceptibility and Immunity.

This work has shown (Section 5) that *Pleospora pomorum* can parasitise at least three varieties of apple (Rival, Wealthy, Allington Pippin), whilst in certain other varieties (Cardinal, Grenadier, Potts's Seedling), originally inoculated with *Pleospora*, *Pleospora* was either not re-isolated (*Polyopeus purpureus* was obtained instead) or was re-isolated in association with other fungi (*Polyopeus purpureus*, *Alternaria grossularieae*, etc.). Considering together the observations noted in Section 4 and the facts recorded in Section 5, the evidence seems to suggest that both *Pleospora pomorum* and *Polyopeus purpureus* exhibit a preference for varieties, but that the varieties preferred by the one are not necessarily those preferred by the other. But the varieties Rival, Wealthy and Allington Pippin, in season from October to December inclusive, were inoculated when unripe whereas Cardinal, Grenadier and Potts's Seedling, in season from August to October inclusive, were inoculated when ripe. Hence the inoculations in the two cases are not strictly comparable since the varieties were not inoculated at the same phase of apple development. The supposition that *Pleospora pomorum* and *Polyopeus purpureus* each exhibit a preference for varieties, for example Rival and Cardinal respectively, is therefore open to the objection that a given variety may be susceptible to one fungus at an early stage of its development and to another at a later stage; in fact, there may be a definite fungal succession. Questions of this kind can only be settled conclusively by carrying out, throughout the season, continuous comparative series of inoculations on specially selected varieties. Certain subsidiary phenomena for example, "arrested spotting" and recrudescence of "spotting" after a period of rest, would then be better understood. Considerable help would be afforded by a parallel study of the seasonal chemical changes taking place in the varieties selected for experimental purposes.

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[1] It is interesting to note in Norfolk Beaufin (Oct.–Dec.) artificially made punctures were not inoculated by the fungus or fungi causing the natural spots formed in October on the inoculated specimen.

Outdoor measures.

The risks of summer infection could be considerably reduced by spraying with Burgundy mixture when the fruit is young. Very probably a weak solution thoroughly applied, similar to that successfully used at Wisley by the authors[1] to prevent the infection of gooseberries by the American gooseberry mildew, would serve the purpose. The treatment should be repeated each year, for until the life-histories of the fungi concerned in "spotting" and the various sources of summer infection are completely known, it is impossible to take comprehensive measures against seasonal recurrence. The success of spraying as a means of control has been repeatedly demonstrated in America by Lamson[2] and others.

Indoor measures.

Summer spraying should practically prevent the appearance of "spotting" in store unless the fungi exist in the fruit-room itself. Where no spraying has been practised, the development of "spotting" could be retarded by storing at lower temperatures than those frequently adopted. It is however eminently desirable to systematically disinfect the fruit-room since some of the fungi enumerated in this paper can grow slowly and even sporulate at a comparatively low temperature (0°–5° C.).

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[1] Horne, Arthur S., in *The Gardeners' Chronicle*, LIX, p. 310 (June 10. 1916); and Horne, Eleanor V., in *The Garden*, LXXXI, No. 2374, 174 (May 19, 1917).

[2] Lamson, W. H. *N. H. Coll. Bulls.* Nos. 27 (Apr. 1895), 45 (May, 1897), 65 (May, 1899), 101 (Apr. 1903).

7. SUMMARY.

This paper presents the results so far obtained in an investigation, which has been carried on since 1915, into "spotting" in apples. The symptoms of "spotting" as they are found and develop in numerous varieties of apple are described. Several fungi have been isolated from spots and cultured in various artificial media with the production of spores.

They include a new genus of Phomatales (*Polyopeus*) and nine new species, of which at least one, *Pleospora pomorum*, as the result of experimental inoculations, has been proved capable of parasitising apples. The fungi do not include any of the species hitherto reported as causal organisms in the United States, the only centre where investigations into the "spotting" of apples, as distinct from the "bitter pit" problem, has been undertaken.

The work was commenced at the Wisley Gardens of the Royal Horticultural Society. During the building of the Society's laboratory it was continued, by the kindness of Professor V. H. Blackman, in the Department of Plant Physiology and Pathology at the Imperial College of Science and Technology. In was later carried on again at Wisley; the work however has been completed at the Imperial College.

The authors' thanks are due to Professor Blackman for his kind help and criticism during the investigation.

A QUANTITATIVE ANALYSIS OF PLANT GROWTH

PART II.

By G. E. BRIGGS, M.A. (Cantab.),
FRANKLIN KIDD, M.A. (Cantab.), D.Sc. (Lond.),
and
CYRIL WEST, A.R.C.Sc., D.Sc. (Lond).

(With 6 text-figures.)

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IV. A Comparison of Assimilation Values determined by the "Growth" Method with those determined by "Gasometric" and "Half-Leaf" Methods 217
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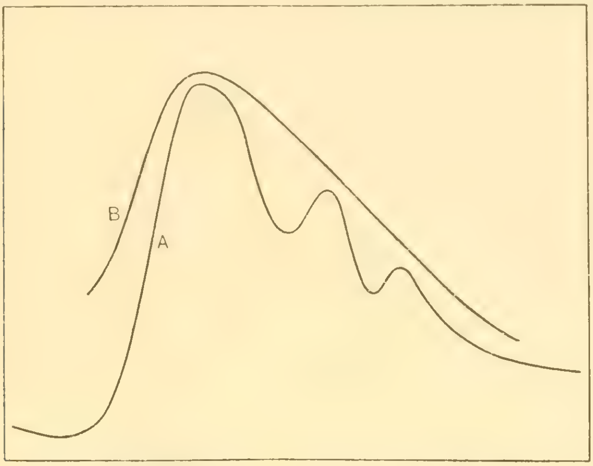
CHAPTER II.

I. Unit Leaf Rate.

In the previous chapter we showed that the Relative Growth Rate curve, that is, the weekly percentage increase in dry-weight plotted against time, for such a plant as maize, has the general form shown in Fig. 1, curve A. Secondly, it was found that the Leaf-Area Ratio curve, that is, the leaf-area per unit dry-weight plotted against time, has the same general form, Fig. 1, curve B. This similarity in the form of the two curves suggests that the weekly increase in dry-weight per unit leaf-area is more or less constant throughout the life-cycle of the plant. In order to ascertain how far this is true we have dealt with the results of Kreusler (13, 14, 15, 16), which were quoted at length in the previous chapter (5), by calculating the values for what we propose to call the Unit Leaf Rate and presenting them for the complete life-cycle of the plant in Unit Leaf Rate curves (Tables I—IV and Figs. 3–6). The Unit Leaf Rate in this paper is the increase in dry-weight per square centimetre of leaf per week, taking as the leaf-area the average of the areas at the beginning and at the end of the week[1].

Before studying these values for Unit Leaf Rate in detail let us consider the possible ideal forms of the Unit Leaf Rate curve. Neglecting the possible effects of environmental factors, if no change occurs in the values of the assimilation and respiration per unit leaf-area the Unit Leaf Rate curve will be a line parallel to the time axis. With regard to assimilation, the activity of the leaves is by no means uniform. The activity of the seedling leaves is smaller than that of the more mature leaves whether carbon dioxide, light, or temperature be limiting, a conclusion which we drew as the result of the analysis of Kreusler's data in the previous chapter, and which has been demonstrated experimentally for some plants by Irving(10) and by Briggs(4)[2]. This change in the



A. Growth-Rate Curve. B. Leaf-Area Ratio Curve.

Fig. 1.

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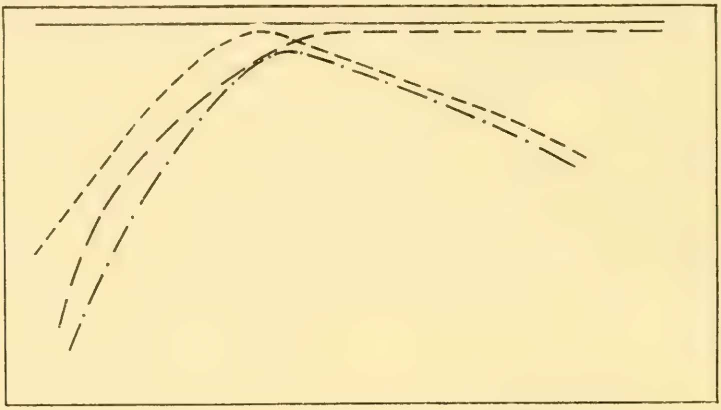
[1] In the appendix to this paper we have put forward two methods of calculating Unit Leaf Rate. Except during the first few weeks it is immaterial which method of calculation is used. During this early period the increase in leaf-area is most probably intermediate between linear and exponential, as an inspection of the figures for leaf-area indicate, and consequently the actual values of the Unit Leaf Rate are intermediate between those calculated by the two methods. The conclusions drawn in this paper are not affected by the method of calculating Unit Leaf Rate, and hence the simpler method is used. The values for Unit Leaf Rate for the year 1877 run as follows: 6·9, 5·6, 5·1, 3·2, 5·8 on the exponential basis and 6·1, 5·1, 4·9, 3·1, 5·7 on the linear basis.

[2] The question of changes in assimilatory activity of the leaf throughout its development, and of young leaves throughout the development of the plant requires more thorough investigation than it has at present received.

assimilatory activity of the seedling leaves would result in an initial rise in the Unit Leaf Rate curve. With regard to respiration, there are two types of changes going on in the plant which tend to alter the respiration of the plant per unit leaf-area as the plant increases in age. First, the dry-weight per unit leaf-area falls in the early stages and then rises until it attains a value about nine times that of its lowest value. The effect of this change, if respiration per unit dry-weight is constant, is to cause a corresponding fall and subsequent rise in the respiration of the plant per unit leaf-area. Secondly, the evidence available is that the respiration per unit dry-weight of the whole plant at constant temperature decreases with age[1]. The effect of this is to accentuate the initial fall and to decrease the subsequent rise just mentioned. The net result of these changes in the rate of respiration per unit leaf-area would therefore be expected to make the Unit Leaf Rate curve still more concave to the time axis (cf. Fig. 2). No quantitative significance is to be attached to these curves which are purely diagrammatic.



———————— on the assumption that assimilation and respiration per unit leaf area are constant throughout.

—— —— —— —— modification allowing for changes in assimilation.

— — — — — — — allowing for changes in respiration.

—— · —— · —— allowing for both.

Fig. 2. Ideal Curves for Unit Leaf Rate.

The actual curves for maize given in Figs. 3–6 show that our expectations are in fact only definitely realised in so far as there are low initial values in all cases. With regard to the main part of the curves the fluctuations are so large that we cannot say more than that the weekly

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[1] Work carried out by the authors shows that such is the case in *Helianthus*.

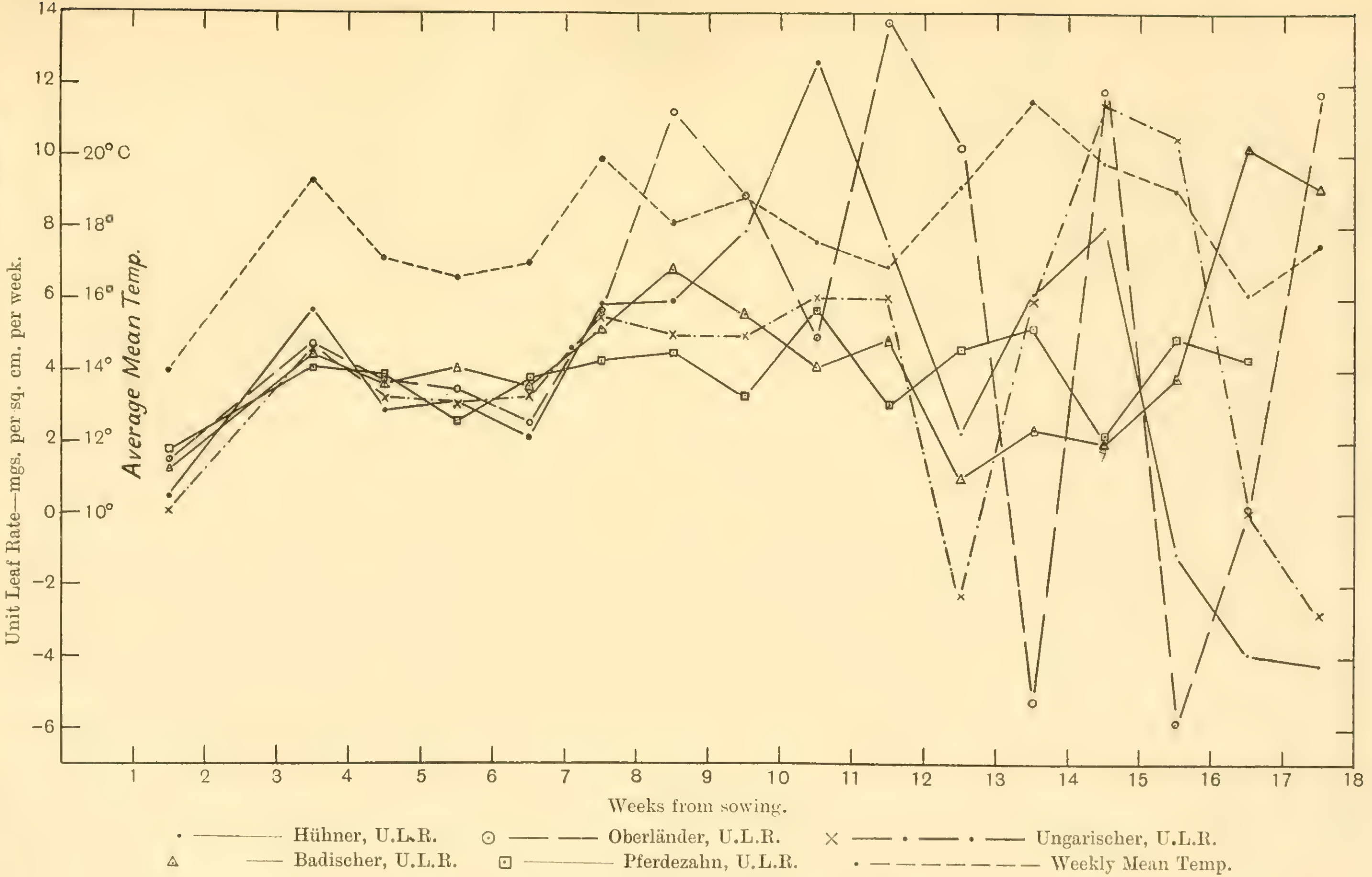


Fig. 3. Five Varieties of Maize — 1875.

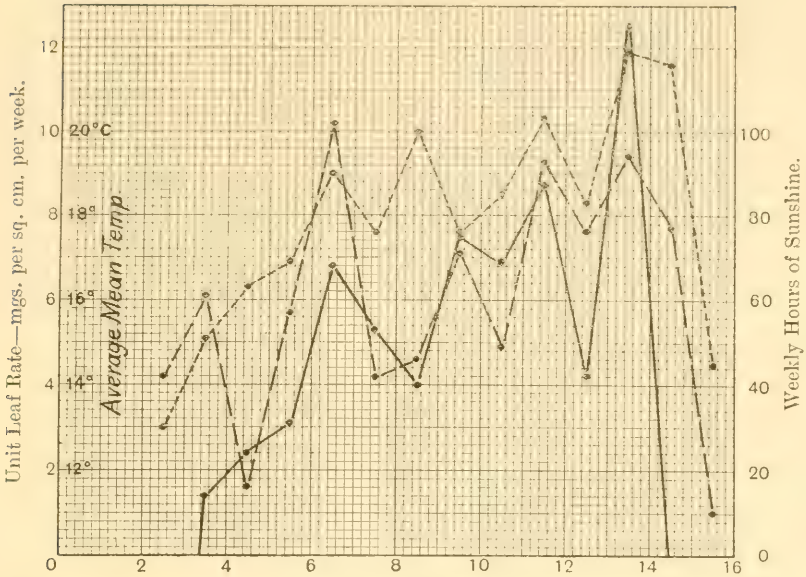
values for increase in dry-weight per unit leaf-area vary more or less about a mean and that the fluctuations attain increasing amplitude as the age of the plant increases. We are led therefore now to attempt to correlate these fluctuations with changes in environmental conditions.

Table I.—*Unit Leaf Rate for five varieties of maize grown at Poppelsdorf in the year* 1875.

Week ending	"Hühner"	"Oberländer"	"Ungarischer"	"Badischer"	"Pferdezahn"	Average mean temperature
1st June	0·5	1·2	·05	1·25	1·8	14° C.
8th ,,	5·7	4·75	4·65	4·45	4·1	19·3
15th ,,	2·9	3·75	3·25	3·65	3·9	17·1
23rd ,,	3·15	3·5	3·1	4·1	2·6	16·6
30th ,,	2·15	2·55	3·3	3·6	3·8	17·0
7th July	5·85	5·7	5·5	5·2	4·3	19·9
13th ,,	5·95	11·2	5·0	6·9	4·55	18·1
21st ,,	7·9	8·9	5·0	5·6	3·3	18·8
27th ,,	12·5	4·9	6·05	4·1	5·7	17·6
3rd Aug.	7·5	13·7	6·0	4·9	3·0	16·9
10th ,,	2·25	10·2	– 2·25	1·0	4·6	19·1
17th ,,	6·1	– 5·2	5·9	2·35	5·2	21·5
24th ,,	8·0	11·8	11·4	2·0	2·2	19·8
31st ,,	– 1·1	– 5·8	10·5	3·8	4·9	19·0
7th Sept.	– 3·9	·15	0·1	10·2	4·3	16·1
15th ,,	– 4·2	11·7	– 2·8	9·1	—	17·5

Table II.—*Unit Leaf Rate for "Badischer Früh" maize* (1876).

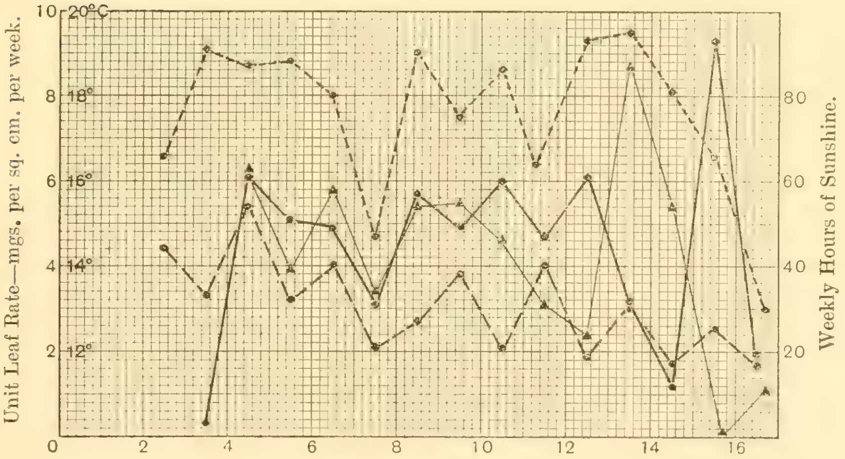
Week ending	Unit leaf-rate	Average mean temperature ° C.	Hours of sunshine
24th May	—	9·8	—
31st ,,	– 10·6	13·0	42
7th June	+ 1·39	15·1	61
14th ,,	2·4	16·3	16
21st ,,	3·05	16·9	57
28th ,,	6·83	19·0	102
5th July	5·36	17·6	42
12th ,,	3·95	20·0	45
19th ,,	7·54	17·6	71
26th ,,	6·87	18·5	49
2nd Aug.	8·5	20·3	93
9th ,,	4·15	18·3	76
16th ,,	12·5	21·9	94
23rd ,,	– 0·46	21·6	77
30th ,,	– 0·43	14·5	10



Weeks from Sowing.

------- Temp. ——- U.L.R. — — — Sunshine.

Fig. 4. Badischer Früh—Mais —— 1876.



Weeks from Sowing.

---------- Temp. — — — — — Sunshine.

• ——— "Nach Auswahl," U.L.R. ▲ "Ohne Auswahl," U.L.R.

Fig. 5. Badischer Früh—Mais —— 1877.

Table III.—*Unit Leaf Rate for "Badischer Früh" maize* (1877).

	Unit leaf-rate (Nach Auswahl)	Unit leaf-rate (Ohne Auswahl)	Average mean temperature ° C.	Hours of sunshine
29th May	—	—	11·9	14
5th June	−15·0	−15·0	16·6	44
12th „	+ 0·23	+ 0·04	19·1	33
19th „	6·1	6·2	18·7	54
26th „	5·1	3·9	18·8	32
3rd July	4·9	5·8	18·0	40
10th „	3·1	3·4	14·7	20
17th „	5·7	5·5	19·0	27
24th „	4·9	5·5	17·5	38
31st „	6·0	4·6	18·6	20
7th Aug.	4·7	3·1	16·4	40
14th „	6·1	2·4	19·3	19
21st „	3·1	8·7	19·5	30
28th „	1·2	5·4	18·1	17
4th Sept.	9·2	− 0·1	16·6	25
11th „	1·9	1·1	13·0	17

Table IV.—*Unit Leaf Rate for "Badischer Früh" maize* (1878).

Week ending	Unit leaf-rate	Average mean temperature ° C.	Hours of sunshine
28th May	—	12·4	—
4th June	—	13·6	40
11th „	−3·55	15·5	27
18th „	+2·25	15·1	19
25th „	4·3	17·9	40
2nd July	6·2	19·8	36
9th „	3·9	17·1	16
16th „	4·3	16·8	20
23rd „	6·4	19·6	57
30th „	6·3	19·8	23
6th Aug.	7·6	18·2	35
13th „	3·9	20·1	32
20th „	5·0	19·3	35
27th „	8·8	17·8	17
3rd Sept.	4·6	19·0	21
10th „	−1·1	19·2	35

II. CORRELATION OF UNIT LEAF RATE WITH ENVIRONMENTAL FACTORS.

(1) *Sampling errors.*

Before attempting to correlate the fluctuations in the values of the Unit Leaf Rate with environmental factors it will be as well to consider to what extent they may be due to sampling errors.

In the case of the results cited above Kreusler states that the seed was selected with care. The weight of the seed seems to have varied, for example, from ·35 to ·45 gm. in the year 1877. He gives no idea as to the coefficient of variation of the samples of seeds nor does he give the coefficient of variation of the dry-weight of the plants for each harvest, but merely the mean value. One cannot therefore say what is the probable error of the figures given for Unit Leaf Rate. Again, the number of plants taken at each harvest seems to have been determined rather by labour involved than by accuracy of results desired. This is perfectly natural when the magnitude of the work is considered. In the case of the earlier harvests about 100 plants were used; this number was reduced to about 40 in the later harvests. The number used for the determination of leaf-area was usually one-half the number harvested.

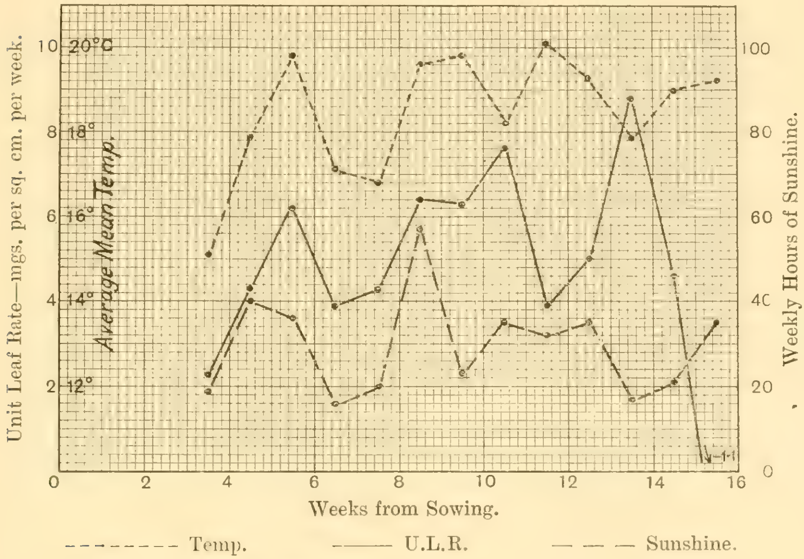


Fig. 6. Badischer Früh—Mais —— 1878.

In order to obtain an idea of the order of probable error to be expected, 40 plants were gathered this year by the authors from an ordinary crop of maize. These gave a mean dry-weight of 6·38 gms. with a probable error of ·25 ±.

In Fig. 3 the Unit Leaf Rate curves for five different varieties of maize grown at the same time under similar conditions are presented. The fluctuations in these curves for the first eight weeks show a good agreement; this may be taken as evidence that the probable error of the mean values up to this stage was sufficiently small not to deprive the fluctuations of significance. The curves A and B, Fig. 5, which are respectively curves for plants selected as mean and for unselected plants of the same variety grown in the same year, add further evidence of the same nature that the results for about eight weeks at the beginning of the life-cycle are comparatively reliable. After the first eight weeks there is no agreement in the fluctuations in the case of the five varieties or in the case of the selected and unselected plants. This lack of agreement may be due in the case of the five different varieties to inherent differences in the plants, and in the case of the selected and unselected to earlier maturity of the unselected. The selected plants were harvested "nach Parcellen," and hence the plants grew in close proximity throughout, whilst the selected ("nach Auswahl") were thinned out at each succeeding harvest.

The following considerations, however, incline us to the opinion that the lack of agreement in the later stages is due partly to sampling error. In the first place, the leaf-area ratio is constantly falling from about the seventh week onwards. For the same coefficient of variation from week to week of the dry-weight of the plants harvested, the probable error of the Unit Leaf Rate will increase as the Leaf Area Ratio falls, provided the Unit Leaf Rate remains roughly constant throughout. We should expect therefore from about the seventh week onwards increasing amplitude of the fluctuations for a given variety, and less agreement in the results from different varieties, as is actually recorded. Secondly, Kreusler's figures[1] show that whenever a decrease in mean dry-weight is recorded a corresponding decrease in leaf-area accompanies it. It is not likely, except at the end of the life-cycle, that either the dry-weight or leaf-area ever decrease to any appreciable extent, still less that they should decrease together. This is an indication that the larger fluctuations in the later part of the life-cycle and the lack of agreement between crops grown in the same year are due to sampling errors.

In attempting to correlate the fluctuations of Unit Leaf Rate with changes in environmental factors we think it advisable, except in the case of the harvests "nach Auswahl," to neglect weeks subsequent to the eighth.

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[1] See tables in previous paper.

(2) *Correlation of Unit Leaf Rate with environmental factors during the early part of the life-cycle*[1].

The environmental factors for which data are given by Kreusler in the different years are as follows (Table V).

Table V.

		Weekly average temperature			Hours of	Total light as sun-hours
Year	Rainfall	Maximum	Minimum	Mean	sunshine	(Besonnungsstunden)
1875	+	+	+	+	–	–
1876	+	+	+	+	+	–
1877	+	+	+	+	+	+
1878	+	+	+	+	+	+

+ means data for this factor are recorded.

In calculating the coefficients of correlation with mean temperature and hours of sunshine the procedure was as follows. In the year 1875, since the weekly Unit Leaf Rates of the different varieties showed very good agreement, the average for the five was taken as expressing the best value. In each year only the values for the five weeks subsequent to the initial rise were used, as the evidence before us indicates that these are least subject to variations due to sampling error. Thus we have a total of 20 cases from which to ascertain the correlation with mean temperature. Since the hours of sunshine were the only record of light intensity for three of the years, the correlation coefficients for the hours of sunshine for the last three years were worked out giving a total of 15 cases.

The correlation coefficients are as follows:

With weekly mean temperature, $r = \cdot 77$.
With weekly mean temperature (years 1876–8), $r = \cdot 64$.
With weekly hours of sunshine (years 1876–8), $r = \cdot 47$.

The partial correlation coefficients for the years 1876–8 are as follows:

With weekly mean temperature, $r = \cdot 53$.
With weekly hours of sunshine, $r = \cdot 24$.

Thus it is seen that the value of the Unit Leaf Rate is governed more by the weekly mean temperature than by the hours of sunshine during the week.

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[1] Since the above was written a paper by Brenchley (3) has appeared in which the writer has investigated the correlation between the rate of growth of garden peas grown in water-cultures and environmental factors. In this paper, however, the rate of growth is expressed per unit dry-weight and not per unit leaf-area as in the above.

(3) *Correlation of Unit Leaf Rate of plants harvested "nach Auswahl" with environmental factors.*

The most complete record of the environmental factors presented by Kreusler for one year is that for 1877, the year in which the selected mean plants were harvested. For this year Kreusler not only gives the usual records, temperature, rainfall, sunshine, and total light, but in a separate paper (12) he gives a very detailed record of the variations in light intensity for each day. The duration of light intensity of the following fractions of full sunlight, ·05, ·1, ·2, ·3 ... 1, is recorded, the duration for each intensity being measured to the nearest five minutes. From these figures we have been able to determine the duration in minutes of all the light above any given intensity for individual days, and hence for individual weeks at the end of which each harvest was taken. These values are presented in Table VI. Kreusler himself determined the "total light-effect" ("Gesammtlichteffekt") by multiplying each light intensity by its duration and summing the results as "Besonnungsstunden." If one attempts to correlate the "total light-effect" with dry-weight increase per unit leaf-area, there is the underlying assumption that this increase is proportional at any moment to the light intensity, that is, is limited by the light intensity throughout. Our knowledge of assimilation would lead us to believe that light limits the rate of assimilation in nature by direct action on the photosynthetic

Table VI.—*Weekly records of light intensity for the year* 1877.

Week ending	Duration in mins. of light 1/20 of sunlight and above	Duration in mins. of light 1/10 of sunlight and above	Duration in mins. of light 2/10 of sunlight and above	Duration in mins. of light 3/10 of sunlight and above	Duration in mins. of light 4/10 of sunlight and above	Duration in mins. of light 5/10 of sunlight and above	Unit Leaf Rate	Hours of sunshine	Total light (in hours)
	* Fractions of duration of light of lower intensities								
19th June	5915	5785	5475	5240	5065	4880	6·1	54	67
26th ,,	6360	6160	5475	5010	4670	4370	5·1	32	54
3rd July	6410	6055	5445	4915	4655	4415	4·9	40	57
10th ,,	6080	5670	5010	4455	4020	3660	3·1	20	41
17th ,,	6620	6190	5580	4995	4560	4210	5·7	27	48
24th ,,	6360	6105	5535	5155	4840	4585	4·9	38	57
31st ,,	6485	6115	5475	4915	4490	4130	6·0	20	46
7th Aug.	5965	5550	4970	4650	4400	4225	4·7	40	56
14th ,,	5550	5370	4955	4450	4060	3725	6·1	19	41
21st ,,	5730	5430	5050	4715	4405	4100	3·1	30	49
28th ,,	5625	5125	4530	4045	3670	3325	1·2	17	35

* For example, in the case of light of 3/10 full sunlight, 2/3 duration of light of 2/10, 1/3 duration of light of 1/10, and 1/6 duration of light of 1/20 sunlight are added.

process only when the intensity is weak, and that normally the factor which limits the assimilatory process is the rate at which the carbon dioxide can reach the chloroplast—the seat of photosynthesis (2). A point to be remembered, however, is that various environmental factors, such as light intensity, temperature, humidity of the atmosphere, etc., may affect the assimilation, not directly by affecting the assimilatory process itself, but indirectly by affecting the degree of stomatal opening and consequently the amount of carbon dioxide which can reach the chloroplast. We have calculated the correlation coefficients between Unit Leaf Rate and the following—

(1) Duration of light above certain intensities plus the duration of weaker lights diminished by factors as stated below.
(2) Total light as calculated by Kreusler.
(3) Hours of sunshine.
(4) Duration of light of all intensities.
(5) Average maximum temperature.
(6) Rainfall.

Correlation coefficients between Unit Leaf Rate and various environmental factors[1].

$r_{L_1} = \cdot 435$
$r_{L_2} = \cdot 60$
$r_{L_3} = \cdot 77$
$r_{L_4} = \cdot 72$
$r_{L_5} = \cdot 67$
$r_{L_6} = \cdot 70$
$r_{L} = \cdot 54$
$r_{L_s} = \cdot 38$
$r_{T} = \cdot 36$
$r_{R} = - \cdot 56$
$r_{R_1} = \cdot 32$

r_{L_1} = correlation coefficient between Unit Leaf Rate and the duration of light, including light down to ·05 sunlight;

r_{L_2} = correlation coefficient between Unit Leaf Rate and the duration of light, including light down to ·1 sunlight plus half the duration of light of ·05 sunlight;

r_{L_3} = correlation coefficient between Unit Leaf Rate and the duration of light, including light down to ·2 sunlight plus half the duration of light of ·1 sunlight plus a quarter the duration of light of ·05 sunlight;

r_{L_4} = correlation coefficient between Unit Leaf Rate and the duration of light, including light down to ·3 sunlight plus two-thirds the duration of light of ·2 sunlight, a third that of ·1 intensity and a sixth that of ·05. And so on for r_{L_5}, etc.;

r_{L} = correlation coefficient between Unit Leaf Rate and total light;

r_{L_s} = correlation coefficient between Unit Leaf Rate and the hours of sunshine;

r_{T} = correlation coefficient between Unit Leaf Rate and average maximum temperature;

r_{R} = correlation coefficient between Unit Leaf Rate and rainfall;

r_{R_1} = correlation coefficient between Unit Leaf Rate and rainfall of the previous week.

[1] The fact that the method of calculation used does not give the exact value for the Unit Leaf Rate during the first few weeks, as already pointed out (see footnote, p. 203), does not materially affect the significance of the correlation coefficients. When the Unit Leaf Rates are calculated on the exponential basis the values for r_{L_3} and r_{T}, for example, become ·76 and ·34 respectively instead of ·77 and ·36.

In calculating these correlation coefficients we have omitted the first phase where the young leaves are most probably assimilating at a much lower rate than the normal leaves, and also the phase marked by the high peak at the end of the life-cycle. In calculating r_{L_1} to r_{L_6} the underlying assumption is that light is not limiting until it is lower than the lowest value before deductions are made. For example, in the case of r_{L_3} it is assumed that light is not limiting the Unit Leaf Rate until the intensity is less than ·3 sunlight and that at lower values the Unit Leaf Rate is proportional to the light intensity. It will be seen that the best correlation is obtained when we make the assumption that light up to one-fifth full sunlight is limiting.

III. CORRELATION OF REAL ASSIMILATION WITH ENVIRONMENTAL FACTORS[1].

We have investigated the question as to how real assimilation per unit leaf-area is correlated with environmental factors. Unit Leaf Rate is the net result of gain due to real assimilation per unit leaf-area plus salt-uptake less loss due to the respiration of the whole plant per unit leaf-area. As the ratio of ash to total dry-weight is of the order of ·06 and undergoes no marked change from week to week (9, 11, 17), the Unit Leaf Rate plus the respiration of the whole plant per unit leaf-area is a fair comparative measure of the real assimilation.

In order to arrive at values for the respiration of maize we determined the respiration of plants about nine weeks old at 2·8°, 10° and 25° C. respectively. The results are given in Table VII.

Table VII.—*Respiration of maize.*

Temperature	Mgs. of CO_2 per gm. dry-weight per hour.
2·8° C.	0·311
10	0·557
25	1·818

From these results we have calculated the loss in dry-weight per unit leaf-area per week on the basis of the average dry-weight and the average leaf-area, and have thus been able to make an estimate of the real assimilation (Tables VIII and IX)[2]. In making this estimate of loss

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[1] Gregory (8) states a few relations between the average rate of assimilation of cucumber plants and the average intensity of radiation, but the figures he gives are too few to establish any general result.

[2] The respiration is calculated for the average mean temperature for the week. Twenty-four hours per day have been allowed.

Table VIII.—*Calculated average weekly values for real assimilation of "Badischer Früh" maize for the year* 1877.

Week ending	Calculated weekly loss in dry-weight of the whole plant due to respiration gms.	Loss per square centimetre per week due to respiration mgs.	Average mean temperature °C.	Average maximum temperature °C.	Calculated real assimilation per square centimetre per week (including salt-uptake) mgs.
19th June	0·071	0·7	18·7	24·4	6·8
26th ,,	0·203	0·6	18·8	23·6	5·7
3rd July	0·495	0·7	18·0	23·4	5·6
10th ,,	0·730	0·5	14·7	18·7	3·6
17th ,,	2·10	0·9	19·0	23·4	6·6
24th ,,	3·52	1·0	17·5	23·3	5·9
31st ,,	6·30	1·5	18·6	22·5	7·5
7th Aug.	7·60	1·6	16·4	21·2	6·3
14th ,,	12·60	2·5	19·3	23·0	8·6
21st ,,	16·80	3·1	19·5	24·7	6·2
28th ,,	15·60	3·5	18·1	22·0	4·7

Table IX.—*Calculated real assimilation for five weeks in early portion of life-cycles.*

Real assimilation mgs. per sq. cm. per week	Average mean temperature	Hours of sunshine	Year
5·2	19·3	—	1875
4·3	17·1	—	,,
4·7	16·6	—	,,
4·2	17·0	—	,,
6·0	19·9	—	,,
3·4	16·3	16	1876
3·9	16·9	57	,,
7·5	19·0	102	,,
5·9	17·6	42	,,
4·8	20·0	45	,,
6·7	18·7	54	1877
5·6	18·8	32	,,
5·5	18·0	40	,,
3·6	14·7	20	,,
6·6	19·0	27	,,
3·2	15·1	19	1878
5·0	17·9	40	,,
6·9	19·8	36	,,
4·5	17·1	16	,,
5·0	16·8	20	,,

due to respiration we have not allowed for the probable falling off in the respiration per unit dry-weight with age, but by taking the values for the respiration of plants of mean age we have done the best we could under the circumstances. The correlation coefficients of real assimilation with various environmental factors are given below.

Correlation coefficients of real assimilation with various environmental factors.

(For years 1875–8.) With weekly mean temperature $r = \cdot 78$
(For years 1876–8.) With weekly mean temperature $r = \cdot 82$
(For years 1876–8.) With weekly hours of sunshine $r = \cdot 60$
(For year 1877, "nach Auswahl.")

$r_{L_1} = -\cdot 07$ $r_{L_4} = \cdot 29$ $r_L = \cdot 17$
$r_{L_2} = +\cdot 08$ $r_{L_5} = \cdot 28$ $r_{L_s} = \cdot 075$
$r_{L_3} = \cdot 28$ $r_{L_6} = \cdot 26$ $r_T = \cdot 56$

The partial correlation coefficients for the years 1876–8 are as follows:

With weekly mean temperature $r = \cdot 76$
With weekly hours of sunshine $r = \cdot 38$

It will be seen that in the case of the five selected weeks for the earlier portion of the life-cycle for the four years the correlation of real assimilation with weekly mean temperature and with hours of sunshine is of the same order as that between Unit Leaf Rate and these two environmental factors, that for temperature being the greater. In the case of the larger portion of the life-cycle of the selected plants for the year 1877 it will be seen that the correlation with light, no matter how measured, is insignificant, whereas the correlation with maximum temperature is considerably greater than it was in the case of the Unit Leaf Rate.

If the allowances made for respiration approach accuracy the indication is that the real assimilation of the plant is not governed by light[1]. Taking into account the whole of the evidence afforded by the correlation coefficients it would seem that the main factor governing real assimilation is temperature. It must be pointed out that the averages of the daily maximum or mean temperatures are not an accurate measure of the average temperature for the days or for the days and nights of the week respectively. The significant correlation of Unit Leaf Rate with temperature may mean, either that it is temperature acting upon stomatal opening or that it is growth (*i.e.* utilization of assimilated material) governed by temperature which controls assimilation. More definite evidence is required before an opinion can be given on this point. We are attempting to obtain such evidence in the case of *Helianthus.*

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[1] If it is found that the apparent assimilation of the leaves is more closely correlated with light than is the real assimilation, then the indications are that light exerts its controlling influence on assimilation under natural conditions, not by acting directly upon the photosynthetic process itself, but indirectly *via* the diffusion stage (stomatal opening, etc.). The data for deciding this fundamental question are not available in the case of maize, but the writers hope to be able to decide this question in the case of *Helianthus* for which they have collected experimental data.

IV. A COMPARISON OF ASSIMILATION VALUES DETERMINED BY THE "GROWTH" METHOD WITH THOSE DETERMINED BY "GASOMETRIC" AND "HALF-LEAF" METHODS.

We have thought it interesting to make a comparison of values of assimilation calculated from results of growth experiments with values obtained by the "half-leaf" method, with leaves attached to or detached from the plant, and by the "gasometric" method with cut leaves.

Unit Leaf Rate, as already stated, is the resultant of the real assimilation, of salt-uptake and of the respiration of the whole plant per cm.^{2} per week. The former takes place only during the hours of light; the two latter proceed during the whole twenty-four hours of each day. If the hours of illumination and the values for the respiration of the leaves and of the whole plant and also the value for salt-uptake are known we can calculate a value for the real assimilation or for the apparent assimilation of the leaves.

In arriving at our estimate of the real assimilation for maize we have used Kreusler's data for the year 1877 since this is the only year for which a full record of the light is available. We have utilised the values of the Unit Leaf Rate for the eleven weeks subsequent to the fourth week from sowing, thus omitting the low initial values, which we have good reason to suppose are not the values for normal leaves, and the exceptionally high value at the end. The results from the "nach Auswahl" experiment were used.

The average Unit Leaf Rate for this period is 4·62[1], and the total hours of light for the eleven weeks number 1118, or a weekly average of 101·7. The total of hours of light after allowance has been made as in column 4, Table VI, is 959, or a weekly average of 87. Using the former value for the light we obtain an average rate for increase in dry-weight per cm.^{2} per hour of light of ·0456, which is equivalent to 3·65 mgs. CO_2 per 50 cm.^{2} per hour. Adopting the other figure for the light we obtain a value of 4·25 mgs. CO_2 per 50 cm.^{2} per hour. Making allowance for the loss by respiration and for the uptake of salts, which for this period shows an average of 6·5 per cent., the real assimilation per 50 cm.^{2} per hour is found to be 4·5 mgs. CO_2 per cm.^{2} per hour when making the assumption that all light is equally efficient, and when light below one-fifth total sunlight is limiting the value becomes 5·3.

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[1] The Unit Leaf Rate calculated on the exponential basis gives a value about 4 % smaller. The real value is intermediate between these two.

Müller (18) has shown by the "half-leaf" method that the apparent assimilation[1] of the leaves of monocotyledons as a class is definitely lower than that of dicotyledons. The values obtained for monocotyledons average about 9 mgs. CO_2 per 50 cm.^{2} per hour[2], the highest being 14 mgs. for *Musa* and the lowest 6·1 gms. for *Cypripedium.* Maize was not used in Müller's experiments. It should be noted that the values given by Müller are average ones determined under varying conditions of illumination, the leaf being left on the plant and translocation being allowed for. It is clear therefore that the value obtained for maize from Kreusler's results, that is, the value obtained for what we propose to call the "growth" method, is distinctly lower than that for monocotyledons as a class determined by the "half-leaf" method. Müller's figures, however, show that in monocotyledons most of the assimilation takes place during the first few hours of illumination and that the rate falls off considerably later. Since his figures are obtained from experiments of only six hours' duration one would expect the value 9 to be much reduced if the experiment had lasted for the whole day.

As Boysen-Jensen (1) came to the conclusion that the values obtained for assimilation by the "gasometric" method give a more accurate value of assimilation under natural conditions than does the "half-leaf" method and since he quotes the results of growth experiments by Weber (21) as confirmatory of this view we think it useful to reconsider this question in the light of other results from growth experiments.

Unfortunately we have no figures for the assimilation of maize determined by the "gasometric" method under natural conditions of CO_2-supply to compare with the results from growth experiments. We can, however, use the results of some growth experiments carried out by ourselves on *Helianthus annuus.* Further, *Helianthus* is a plant which has received a good deal of attention, both "gasometric" and "half-leaf." The results are given in Table X.

It will be seen that the results obtained for assimilation with *Helianthus* by the "gasometric" method are of the same order as the results

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[1] Müller's figures do not take into account the respiration of the leaf; this, however would make very little difference.

[2] The value for CO_2 is calculated as 8/5 of the increase in dry-weight.

Table X.—*Values for assimilation determined by different methods.*

Method	Investigator	Plant	Light	Temperature	Period	Remarks	Value obtained for assimilation mgs. CO_2 per 50 sq. cm. per hour
"Growth"	Kreusler (13, 14, 15, 16)	Maize	Total duration of illumination	Changing	11 weeks	Respiration of plant and salt-uptake allowed for	4·5
,,	Weber (21)	*Helianthus annuus*	10 hours per day	,,	50 days	,,	4·4
,,	Present writers	,,	Total duration of illumination	,,	1 week	Respiration of plant, but not salt-uptake allowed for	8·5
"Gasometric"	Giltay (7)	,,	Changing	13°–27° C.	Few hours	At Wageningen. Apparent assimilation	2·9 (average) 3·8 (maximum)
,,	,,	,,	,,	28°–36° C.	,,	At Buitenzorg. Apparent assimilation	3·9 (average) 7·2 (maximum)
,,	Brown and Escombe (6)	,,	Diffuse light	20° C. (*circa*)	,,	Apparent assimilation	3·4
,,	Boysen-Jensen (1)	*Sinapis*	Excess light	20° C.	,,	Real assimilation	6·0
"Half-leaf"	Sachs (19)	*Helianthus*	Sunlight	25° C.	—	Cut leaves. Apparent assimilation	13·0 (maximum)
,,	Müller (18)	,,	Illumination changing	15·8°–23·4° C.	—	On plant (translocation allowed for). Apparent assimilation	14·0 (average)
,,	,,	*Allium*	,,	,,	—	,,	9·0 (average)
,,	Thoday (20)	*Helianthus*	Sunlight	27°–29° C.	—	Cut leaves. Apparent assimilation	9·0 (average) 13·0 (maximum)

obtained by Weber by the "growth" method, but are distinctly lower than those obtained by the present writers by the same method. Weber's experiments, however, are open to criticism on the ground that his plants were grown in pots, under which condition *Helianthus* does not flourish, and moreover, they were grown in a greenhouse where the light would be considerably less than that under natural conditions. Our value 8·5 is based on experiments carried out under natural conditions. For a certain week, *i.e.*, the fourth from germination, the Unit Leaf Rate was found to be 9·0. During this week the respiration was measured continuously. When allowance is made for the loss in dry-weight due to respiration the value for assimilation becomes 12·3. The real value would probably be slightly higher since the respiration of a plant exposed to the direct rays of the sun would be higher on account of increased temperature—the temperature of our respiration experiments was the shade temperature. The hours of light for this week numbered 116[1]. Utilising this figure for the hours of light we obtain a value of 8·5 mgs. CO_2 per 50 cm.^{2} per hour of light. This value 8·5 includes salt-uptake, which at the most would not be more than 7 per cent., thus it is shown definitely, for *Helianthus*, that the values estimated by the "gasometric" method, which moreover does not include the hours of faint light in the earlier part of the morning and in the later part of the evening, do not give a reliable estimate of the assimilation which the plant can carry out under natural conditions. Our figure of 8·5 is smaller than the figure obtained by the "half-leaf" method.

We propose to consider on a later occasion the probable reason for the "growth" method giving lower values than does the "half-leaf" method.

V. SUMMARY.

In this chapter we have continued our analysis of the results of the experiments on the growth of maize carried out by Kreusler and his co-workers. The rate of growth has been expressed per unit leaf-area instead of per unit dry-weight as in the last chapter. The term "Unit Leaf Rate" is used for the weekly rate of increase of dry-weight in mgs. per sq. cm. The Unit Leaf Rate, instead of undergoing a perfectly definite type of variation, as does the Relative Growth Rate, fluctuates about a mean value. The larger fluctuations which occur in the values for Unit

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[1] If it is assumed that light below 1/3 sunlight is limiting, the hours of light become 88 and the value for assimilation 11·2.

Leaf Rate calculated for the later phases of the life-cycle have been attributed mainly to sampling errors.

Correlations between Unit Leaf Rate and various environmental factors have been determined.

The general evidence is that the Unit Leaf Rate is correlated more closely with temperature than with any of the other environmental factors.

By allowing for respiration on the basis of our own experimental results values for the real assimilation were arrived at. These also show a closer correlation with temperature than with light.

The values for assimilation determined from the Unit Leaf Rate are of a lower order than those determined by the "half-leaf" method, but much higher than those determined by the "gasometric" method.

Finally, the authors wish to express their indebtedness to Dr F. F. Blackman for his stimulating criticism and help in this and in the previous chapter.

(*To be continued.*)

APPENDIX.

The definitions and inter-relation of the terms used by the present writers in their analysis of plant growth are as follows (22):

The *relative growth-rate*, R, is the weekly percentage rate at which the dry-weight increases. It may be assumed for purposes of calculation that the increase from week to week takes place exponentially, $\frac{R}{100}$ being the exponent, or that it takes place linearly. Both are approximations. If W be the dry-weight $\frac{dW}{dt} = \frac{RW}{100}$. This formula expresses the relation between R and W assuming the increase takes place exponentially and when integrated the equation becomes $\log_e W_2 - \log_e W_1 = \frac{R}{100}$, where W_2 is the dry-weight at the end of the week, W_1 at the beginning of the week and e the base of the natural logarithms. If it is assumed that the increase is linear $\frac{R}{100} = \frac{W_2 - W_1}{\frac{W_1 + W_2}{2}}$.

Leaf-area ratio, A, is the ratio of leaf-area to dry-weight, that is $\frac{L}{W}$. For simplicity $\frac{L_1 + L_2}{W_1 + W_2}$ is used when making calculations on the linear basis, L_1 being the leaf-area at the beginning of the week, and L_2 at the end of the week.

Unit leaf-rate, E, is the rate of increase in dry-weight per unit leaf-area per week. Then $\frac{dW}{dt} = EL$ and if the exponential basis be adopted for both leaf-area and dry-weight increase then

$$E = (\log_e L_2 - \log_e L_1) \frac{W_2 - W_1}{L_2 - L_1}.$$

On the linear basis $E = \frac{W_2 - W_1}{\frac{L_1 + L_2}{2}}$, that is, the weekly increase in dry-weight divided by the average leaf-area.

Relative leaf growth-rate, R_L, is analogous to relative growth-rate and

$$\frac{R_L}{100} = \log_e L_2 - \log_e L_1, \quad \text{or} \quad \frac{L_2 - L_1}{\frac{L_1 + L_2}{2}},$$

according to whether the calculations assume an increase on the exponential or the linear basis.

An inspection of the above definitions and formulae will show that whichever formal conception as to the mode of increase of dry-weight and leaf-area be adopted the Relative Growth Rate is merely the product of the Leaf-area Ratio and the Unit Leaf Rate multiplied by 100. This will be made clear by the following. On the exponential basis

$$R = 100 \frac{\frac{dW}{dt}}{W}, \; A = \frac{L}{W}, \text{ and } E = \frac{\frac{dW}{dt}}{L}, \text{ hence } R = 100AE.$$

On the linear basis it will be seen that the same relationship holds.

In the present and the previous chapter the linear basis has been adopted as the simpler one, and as being sufficiently accurate for the purposes.

None of the above formulae involves the assumption that R, R_L, A, or E are constant throughout the life-cycle.

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DOUBLE CROSS-GRAIN.

By J. F. MARTLEY.

(With Plate XIII and 11 text-figures.)

There is a certain amount of ambiguity in the meaning of the term cross-grain as applied to wood owing to it being used to describe conditions of grain which are similar in appearance though due to different causes.

The simplest use of the term is in its application to a plank sawn obliquely to the longitudinal axis of a straight grained log. A similar condition of the grain can be seen in planks, especially in the outer ones, which have been sawn from logs of considerable taper.

A more logical use of the term is in the description of planks sawn from a torse or spiral-grained log, for in this case it is impossible to saw a plank without cutting across the grain.

There is still a further type of cross-grain, seen in many timbers native to hot climates, which might be called interlocked or double cross-grain, the investigation of which forms the subject of the present paper.

This grain can often be recognised by a characteristic banded appearance on radial surfaces, due to differences in the reflection of light from a number of zones parallel to the longitudinal axis of the trunk. When such a wood is planed, it is at once evident that the grain in alternate zones is inclined in opposite directions.

This variation in the inclination of the grain can also be demonstrated by making successive tangential splits in a narrow stick sawn transversely off the end of a radial board, when it will be found that the inclination of the grain swings alternately to the left and right of the straight.

In the absence of any specific investigation, the simple spiral grain of torse wood suggested that the grain of these exotic timbers is of the nature of a double spiral, the inclination of the grain alternating with the growth of the tree between a left-handed and a right-handed spiral. It was on this supposition that Professor Groom based the explanation of the warping and twisting phenomena of the dipterocarpous wood called Yang (1).

In order to continue his work on the warping and twisting phenomena shown by these woods and to investigate their structure Professor Percy Groom secured through the kindness of Mr R. S. Pearson, Imperial Forest Economist, India, portions of the trunks, in the form of cylindrical drums several feet or more in length, of the undermentioned Indian trees. These Professor Groom entrusted to me to make this preliminary investigation into the true nature of this type of cross-grain:

Flacourtia Cataphracta Roxb.	Bixaceae.
Pentacme suavis D.C.	Dipterocarpaceae.
Shorea robusta Gaertn.	,,
Pterospermum acerifolium Willd.	Sterculiaceae.
Garuga pinnata Roxb.	Burseraceae.
Chloroxylon Swietenia D.C.	Meliaceae.
Cedrela Toona Roxb.	,,
Pterocarpus Marsupium Benth.	Leguminosae.
Ougenia dalbergioides Benth.	,,
Dalbergia Sissoo Roxb.	,,
,, *latifolia* Roxb.	,,
,, *Oliveri* Gamble.	,,
Xylia dolabriformis Benth.	,,
Hardwickia binata Roxb.	,,
Anogeissus latifolia Wall.	Combretaceae.
Schrebera swietenoides Roxb.	Oleaceae.
Gmelina arborea Linn.	Verbenaceae.
Mallotus philippinensis Muell.	Euphorbiaceae.
Holoptelea integrifolia Planch.	Ulmaceae.

Before I received the material each drum had been sawn up into a number of half-inch boards of which only two at the most were truly radial. In addition there was a transverse disc, a little over an inch thick, for each species, but there was nothing to indicate whether the disc and drum had been contiguous, or separated, in the log from which they had been sawn.

METHODS OF INVESTIGATION.

The methods of investigation into the course of the grain can be classified under two headings, namely: (1) Preliminary Investigations, and (2) Detailed Investigations. The former deal with the methods of attacking the problem, while the latter are concerned with the actual investigation.

Preliminary Investigations.

As the edges of the boards had not been trimmed off except in *Albizzia procera*, it was an easy matter to assemble the boards and examine the grain on the reconstructed drums.

The species could be separated into two groups according to the grain shown on the surface of the drums but it was impossible to say how far this grouping would hold good for complete trunks.

I. **Grain of uniform inclination.**

Garuga pinnata came under this heading with a left-handed spiral grain.

Albizzia procera, as far as could be judged, also came under this heading with a straight grain.

Calophyllum sp. (Poon). An examination of a six-foot beam suggested that Poon should be included in this group.

II. **Grain of variable inclination.**

On the surface of some sectors of a drum the grain might be straight, on others inclined as a right-handed or left-handed spiral and again on others the grain might have a sinuous or serpentine course. The general direction of the grain where it was serpentine was either parallel or inclined to the axis of the trunk. Unlike the other group, there was no transverse level where the grain was uniformly inclined around the circumference.

All the remaining eighteen species came into this group, differing from each other in the degree of inclination shown by the grain and in the length of the undulations where the grain was serpentine. The drums were too short to find the average length of the undulations in the different species. The shortest undulations seen measured between six inches and a foot in length.

Each species had next to be tested for the occurrence of cross-grain, which could readily be demonstrated by taking a narrow stick sawn transversely off the end of a radial board and splitting it radially down the centre.

The fracture on the transverse surface under the edge of the splitting instrument will naturally be straight but the fracture on the transverse surface, the reverse to the one struck, will be sinuous, the departures from the straight conforming to the variations in the inclination of the grain since the plane of fracture follows the inclination of the grain.

A radial stick from each species was treated in this manner and direct

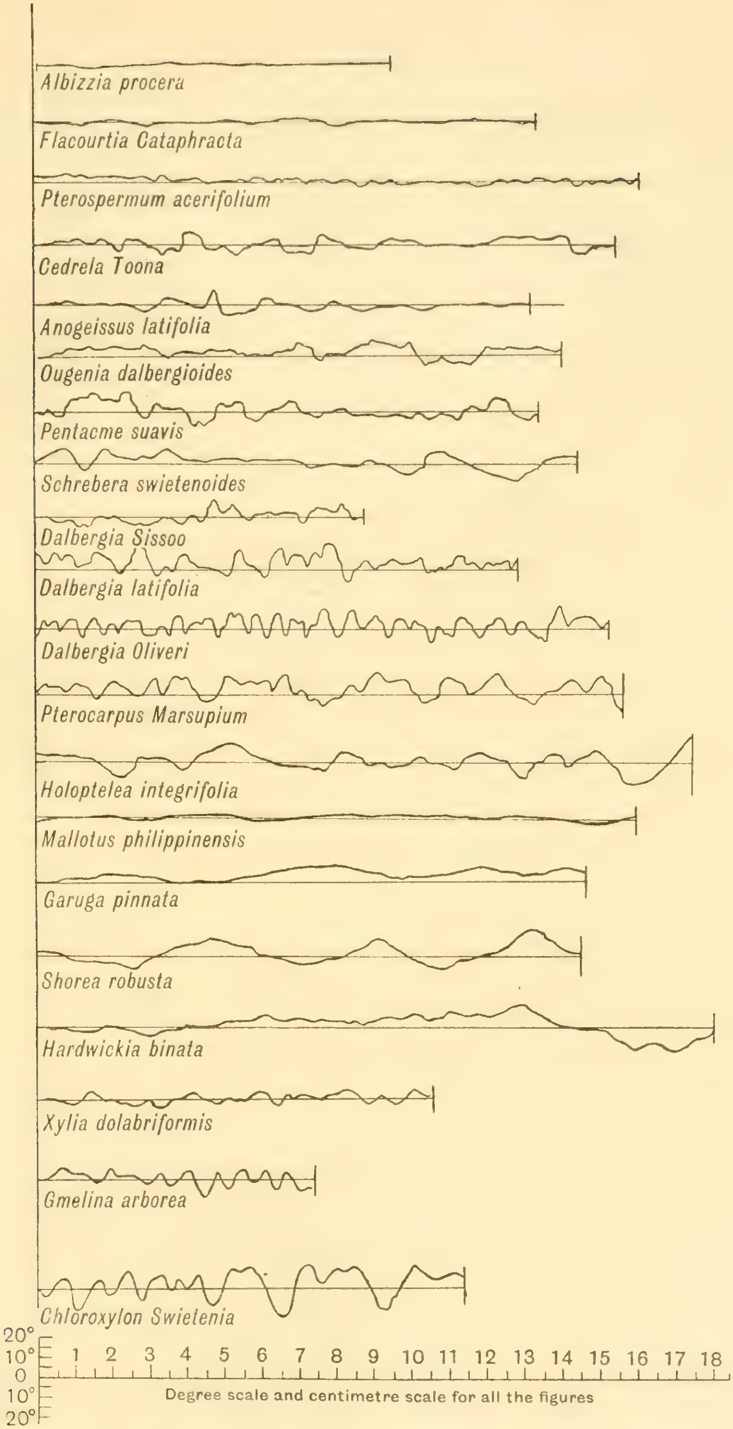

Albizzia procera
Flacourtia Cataphracta
Pterospermum acerifolium
Cedrela Toona
Anogeissus latifolia
Ougenia dalbergioides
Pentacme suavis
Schrebera swietenoides
Dalbergia Sissoo
Dalbergia latifolia
Dalbergia Oliveri
Pterocarpus Marsupium
Holoptelea integrifolia
Mallotus philippinensis
Garuga pinnata
Shorea robusta
Hardwickia binata
Xylia dolabriformis
Gmelina arborea
Chloroxylon Swietenia
20°
10°
0
10°
20°
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Degree scale and centimetre scale for all the figures

Fig. 1. Outline of a radial fracture for each species obtained from a stick an inch broad, sawn transversely off the end of a radial board.

tracings of the fractures obtained are reproduced in Fig. 1. An examination of the tracings shows that there are all types of gradation from the approximately straight grain of *Albizzia procera* to the uniform type of the double cross-grain characteristic of *Shorea robusta*.

The differences in the character of the cross-grain of the various species appear to be of a quantitative rather than of a qualitative nature, depending on the degree of regularity in the changes in the inclination of the grain, on the average radial distance between the successive right-handed and left-handed phases and on the average angle included between the maximum left-handed and right-handed inclinations of the grain.

The splitting of a radial stick provides a ready means of demonstrating changes of inclination in the grain for a very limited portion of the trunk, but in order to obtain a satisfactory insight into the variations in the inclination of the grain it is essential to know what the appearance of the grain would be like on the surface of the woody cylinder at successive intervals during the life of the tree.

The presence of clearly defined "growth-rings" greatly facilitated this investigation for, on the assumption that they delineated tissues produced at the same time, these rings supplied the necessary time unit without which it would have been impossible to proceed.

In order to obtain a general idea of the course of the grain in a drum use was made of these rings in the case of *Xylia dolabriformis* by splitting successive collars from off the disc at every fifth ring, and by careful planing of a radial board tangentially to the rings. In both cases the inclination of the grain was noted on the successively exposed surfaces.

It was not possible to make detailed records of the variations seen in the inclination of the grain, but the general impression obtained was that there were alternate right-handed and left-handed phases of inclination throughout the drum and that the conformation of the grain on the surface of the woody cylinder was at all times of the type already described under Group II, since, in the radial plane, the grain was often serpentine, its general direction alternating between left-handed and right-handed, and because around any ring in the transverse disc, the grain was never uniformly inclined although its inclination alternated with growth between wholly right-handed and wholly left-handed.

Before proceeding with the detailed method of investigation, a digression is necessary in criticism of the assumption that the rings of these Indian timbers are of the nature of growth-rings.

In dicotyledonous trees, native to temperate climates, the rings are defined by one or more of the following structural characters (see Groom (2)).

(1) Variation in the size of the vessels (Oak, Ash).
(2) Variation in the distribution of the vessels (Apple, Hawthorn).
(3) Decrease in the radial dimensions of one or more layers of wood elements (Sycamore, Poplar).
(4) Local decrease in the radial dimensions of the ray cells (Oak, Poplar).
(5) Local broadening of the rays (Oak, Beech).
(6) Presence of a more or less continuous sheet of parenchyma (Poplar).
(7) One or more layers of cells with darker contents.

Where the size and distribution of the vessels is uniform or nearly so and the remaining characters are ill-defined, it is often difficult to recognise a structural limit to the ring under the microscope, although rings can be recognised by the naked eye. This is the case with Boxwood and, to a lesser extent, with Pearwood.

Experience has shown that these rings are annual and are correlated with leaf fall and cessation of active growth before the cold weather sets in, and with the production of fresh foliage when conditions are again suitable for the assumption of growth in spring time.

All the Indian timbers examined in the course of this investigation showed concentric rings which, to the eye, were as well defined as those of many temperate climate trees.

In none of the species examined by the detailed method did the size or distribution of the vessels play any part in the definition of these rings, thus resembling the Willows, Poplars, and Horse Chestnut of this country.

The structural definition of the rings of these species, based on a limited number of sections, was as follows:

In *Chloroxylon Swietenia* the rings were very clearly defined by a layer or sheet of parenchyma two or three cells deep characterised by numerous simple pits.

In *Shorea robusta* the rings were defined by a sheet of parenchyma three or four cells deep. A slight tangential broadening of the rays was apparent where they passed through this sheet. Cysts or canals, probably of schizogenous origin, were of frequent occurrence in this layer.

The ring in *Hardwickia binata* was defined by a layer, three to six cells thick, consisting of parenchyma and of elongated narrow-lumened cells with brown, resinous looking contents. The walls of the elongated cells were thickly sprinkled with numerous fine pits.

In *Xylia dolabriformis* a layer, one or two cells deep, with darker contents, and apparently fibrous, bounded the rings.

The structural definitions of the rings in *Gmelina arborea* was much less distinct than in the other species although the rings themselves were apparent to the eye. An indistinct layer of parenchyma appeared to delineate the rings.

With regard to the relation between seasonal changes and the periods of growth of these trees, the following information was obtained from Brandis (3):

Chloroxylon Swietenia. Common in the deciduous forests of the Western Peninsula. Flowers March to April. Leaves renewed in May.

Shorea robusta. Never quite leafless. The young foliage appears in March with the flowers.

Hardwickia binata. ——

Xylia dolabriformis. Flowers while leafless, in March and April.

Gmelina arborea. Leaves shed from February to April. New foliage appears in May. Flowers from February to April, generally before the leaves are out.

Calophyllum sp. (Poon). Evergreen forests.

Similar seasonal changes are also recorded for the greater number of the remaining species.

The similarity, with regard to the structure of the rings and to the response to seasonal changes, between the Indian trees and the trees of temperate climate indicates that the rings shown in the Indian timbers are of the nature of growth-rings correlated with seasonal changes and lends support to their use as indices of contemporaneity.

Detailed Investigation.

The object of the method adopted was to find the inclination of the grain in every growth-ring of the trunk and to study how the inclination varied from ring to ring.

With the material to hand it was only possible to do this for one transverse and one radial plane of the drum, nevertheless, the data obtained were sufficient for forming a clear idea of the changes which the course of the grain underwent during the growth of the tree.

The rings were counted on the transverse disc of each species examined, and, to ensure correspondence in numbering along the different radii, the rings were followed completely round the disc. In places where the rings were indistinct, only the more prominent were traced round while the space between two such prominent rings was divided into a convenient number of equal subdivisions.

Where the growth of the tree did not show any great irregularities there would be little error in the contemporaneity of these "pseudo-growth rings" along the different radii of the disc.

After the rings had been counted and numbered, a number of sticks, usually eight in all and at an angle of 45 degrees to each other, were sawn radially out of the discs, care being taken to make the sides of the sticks as near as possible perpendicular to the surface of the disc. The sticks sawn from the disc constituted the transverse series for that species.

The longitudinal series were prepared by sawing a radial board of each species transversely into a number of sticks an inch in depth. The rings were counted on the corresponding transverse surfaces, differences of width and of tint ensuring correspondence in the numbering of the rings in the sticks of each longitudinal series.

Subsequent to the measuring of the width of the rings, the sticks of each transverse and longitudinal series were submitted to the following treatment.

By using a knife each stick was divided up into a number of thin slips by splitting parallel to the rings. So far as the width of the rings permitted a division was obtained between each ring, and in the broader rings as many as three or four splits were easily made. In order to prevent confusion the number of the ring was marked on each slip, a precaution necessitated by the large number of slips obtained from each stick.

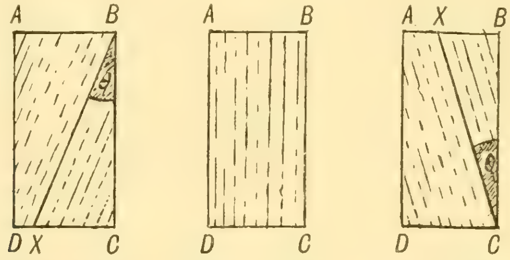
The inclination of the grain was then measured on the outer tangential face of the slips and tabulated in conjunction with the width of the rings for each stick.

Lettering the outer face of a slip as in Fig. 2 the grain was traced by means of a lens and a fine needle from the top corner (B) or bottom corner (C) of the right-hand side BC, according to whether the inclination of the grain was right-handed or left-handed, to where it met the opposite side, CD or AB as the case might be, at the point X. By measuring XC or XB and the side BC with a micrometer screw, the angle of inclination of the grain (θ) to the straight could readily be calculated from the tangent.

The inclination of the grain was said to be right-handed and denoted by the sign "/" in the tables when it passed from the top right-hand corner toward the bottom left-hand corner; when it was inclined in the opposite direction it was said to be left-handed and denoted by the sign "\\". When the grain was parallel to the reference side *BC* it was called straight and was represented in the tables by the letter "*v.*"

The inclination of the grain might equally well have been calculated with the left-hand side, *AD*, of the slips as a basis but for the sake of uniformity measurements were made from the right-hand side only.

The changes in the inclination of the grain along each stick were next plotted diagrammatically in the form of a curve. The rings were plotted along a horizontal line according to their width in centimetres to a scale of 2 to 1. To a scale of 1 mm. to a degree, the inclination of the grain at each ring was plotted in its correct position about the horizontal line, degrees of right-handed inclination being plotted above the line, and degrees of left-handed inclination below the line. When the grain was straight the point was plotted in its correct position on the line itself.



Right handed inclination　*Straight grain*　*Left handed inclination*

Fig. 2. Method determining the inclination of the grain.

On joining these points together a curve was obtained which showed at a glance both the inclination of the grain and the rate of change in the inclination of the grain at any ring.

In order to represent diagrammatically changes in the course of the grain in a radial plane the curves showing the changes in the inclination of the grain along the sticks of the longitudinal series were placed in sequence one above the other. The same procedure was adopted with the curves of the transverse series. On combining the results obtained from the examination of the transverse and longitudinal series of curves a comparatively clear mental picture was obtained in each species examined of the changes in the course of the grain during the life of the tree.

In order that the individual curves of a series should be more readily comparable among themselves the growth-rings were plotted for all the curves according to their width along a stick of intermediate length. In the longitudinal series this procedure produced no distortion of the curves since in all the species examined the width of the rings remained practically constant through the series, but in the transverse series, on the other hand, a distortion of some of the curves would be caused where the growth of the tree had been excentric. This distortion however will not affect the value of the curves for comparing changes in the inclination of the grain.

In order to test the reliability of the results obtained by this method of investigating the course of the grain, recourse was had to an elaboration of the method of radial fracture already described under the head of "Preliminary Investigations" as the most convenient method for demonstrating double cross-grain.

For checking the longitudinal series of curves, a radial board, if possible adjacent to the one which supplied the material from which the changes in the course of the grain in the longitudinal direction had been derived, was sawn transversely into a number of sticks an inch broad. For ease in subsequent comparison several of the more prominent rings were inked in on the corresponding transverse surfaces of the sticks. Each stick was then split radially, the direction of the split being made in the same sense in each stick. When the sticks were placed in sequence side by side a series of curved fractures was shown which, though not always identical in form, corresponded very closely with the longitudinal series of curves of the same species.

Prior to describing the course of the grain in the different species, it is advisable to mention the errors to which the method of investigation is subject and to estimate their probable effect on the results obtained.

The use made of the rings as an index of contemporaneity has already been discussed. The distinctness with which the individual rings could be followed round the discs and through the longitudinal series reduced errors in the numbering of the rings to a negligible minimum in all except the transverse series of *Gmelina arborea*.

In the actual measurement of the inclination of the grain on the slips repeated tests showed that errors from this source were not likely to have exceeded one degree.

Where the radial board had not been sawn parallel to the axis of the tree a uniform left-handed or right-handed bias in inclination would be given to the grain as a whole. In no case was there any appreciable inclination between the radial board and the axis of the trunk and in any case provided such inclination was not excessive, the comparative value of the curves would not be influenced since each stick would be equally affected.

The sticks of the transverse series were subject to a similar type of bias which was, however, of a two-fold origin; first to the possibility of the disc not being truly at right angles to the longitudinal axis and secondly to the sides of the sticks not being accurately perpendicular to the transverse surface.

The errors due to the first cause were considered to be negligible, since, as far as could be judged, a disc was never inclined at more than about five degrees to the transverse. The inclination between the sides of the different sticks of a transverse series varied within a range of three degrees at an outside estimation.

As in the longitudinal series errors due to these causes will not affect the comparative value of the curves so far as changes in inclination of the grain are concerned and need only be borne in mind when comparing the inclination of the grain at different points.

As to the sense in which various terms are used the words "Period length," "Amplitude" and "Phase" are employed with meanings analogous to those they possess when used in Physics for the description of wave motion.

The period length is the radial distance between the two maximum inclinations which delimited the period. Amplitude is the angle included between a maximum right-handed and left-handed inclination of the grain. As each period comprises a right-handed or left-handed swing of the grain which are only rarely of equal amount, the average of the two swings is taken as the amplitude of the period. It was on this basis that the ratio of period length to amplitude was worked out.

SHOREA ROBUSTA.

The data regarding the width of the growth-rings and the inclination of the grain at the various rings, from which the two series of curves (Figs. 3 and 4) were constructed are tabulated for the sticks of the transverse and longitudinal series in Tables I and II respectively.

Although in both series the rings were counted from the centre, the numbering of the rings in the two series does not correspond, there being fewer rings in the longitudinal series. This discrepancy is due to two

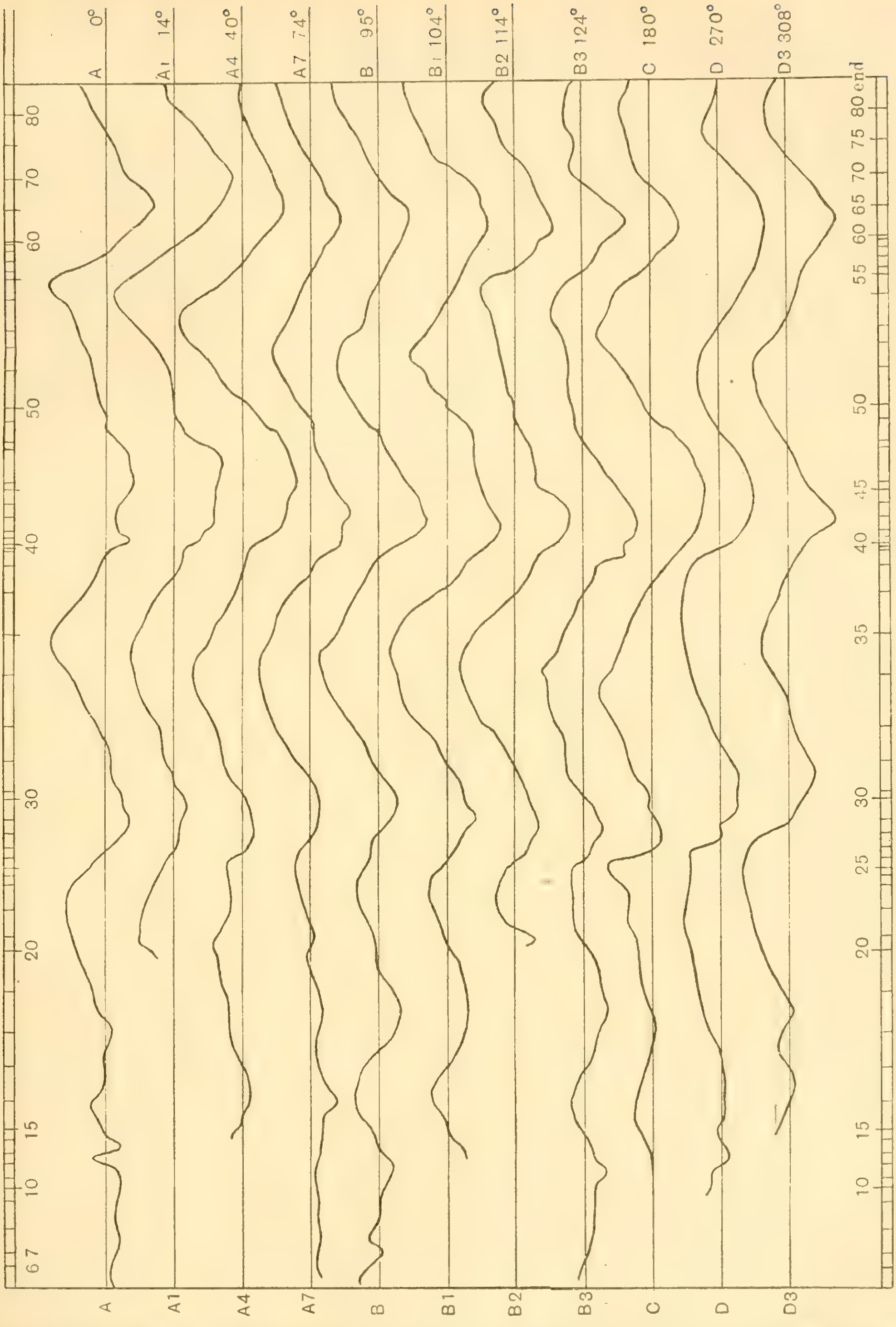


Fig. 3. *Shorea robusta.* Transverse series. The individual curves show the inclination of the grain at the successive rings along the different sticks. The number against each curve gives the angle between that stick and stick A. In each curve degrees right-handed inclination plotted above the base line and degrees left-handed inclination below. Scale: rings plotted to a scale of 2 cm to 1, and inclination of the grain 1 mm. to 1 degree.

Table I. *Shorea robusta.* Transverse series.

The first column of each stick gives distance of each ring in centimetres from the centre, and the second column inclinations of the grain in degrees in the different rings. Where the rings were broad three readings could be taken at the beginning, middle and end of the ring. Straight grain denoted by "*v*," right-handed inclination by "/" and left-handed inclination by "\."

No. of ring	A				A 1				A 4				A 7				B				B 1			
Centre	0 cms.		—		0 cms.	0			0 cms.		.		0 cms.		.		0 cms.		.		0 cms.			
1	.		..		.	.			.		.		.		.		.		.		.			
2	.		—		.	.			.		.		.		.		.		.		.			
3	.		*v*		.	.			.		.		.		.		.		.		.			
4	.		3 \		.	.			.		.		.		.		.		.		.			
5	1·10		1½\		.	.			.		.		1·80		3 \		2·00	6 /	6 /	.	.			
6	1·30		2½\		.	.			.		.		2·10		2 \		2·28	1½/	1 /	.	.			
7	1·80		4 \		.	.			.		.		2·60		3 \		2·59	½\	3 /	.	.			
8	2·15		3 \		.	.			.		.		2·90		2 \		2·85	½/	½\	.	.			
9	2·25		4 \		.	.			.		.		3·05		2½\		3·25	½\	.	.	.			
10	2·45		4½\		.	.			.		.		3·25		1½\		3·45	1½\	.	.	.			
11	2·60	.	3 \	.	.	.			.		.		3·50		.		3·60	4 \	.	.	.		.	
12	2·85	*v*	4 /	.	.	.			.		.		3·60		2½\		3·80	3½\	.	.	3·25		5½\	
13	3·30	3 \	4½\	1½\	.	.			.		.		3·70		.		3·95	*v*	.	.	3·45		4 \	
14	3·95	.	*v*	.	4·15	.			.	.	.	3	3·80		.		4·15	1½/	.	.	3·60		*v*	
15	4·20	.	2½/	4 /	4·35	.			4·45	*v*	*v*	1½\	3·90	3½\	3½\	7½\	4·30	2½/	6 /	.	3·75		1 /	4 /
16	4·60	.	*v*	.	4·65	.			5·10	2 \	2 \	*v*	4·65	7 \	4 \	*v*	4·70	.	6 /	5 /	4·10		4 /	½/
17	5·00	.	*v*	.	4·80	.			5·65	.	2½	.	5·15	.	.	2 \	5·18	.	*v*	4½\	4·55		3½\	5 \
18	5·19	1½\	2½/	2½/	5·15	.			5·85	3 /	3½/	4 /	5·75	.	4 \	2½\	5·70	.	6½\	5½\	5·15		6½\	6 \
19	5·90	.	6 /	.	5·90	.			6·45	6 /	6½/	7½/	6·35	.	*v*	*v*	6·30	.	*v*	½/	5·70		4 \	2 \
20	6·45	.	9 /	.	6·55	6½/	10 /	.	7·20	8½/	—	7½/	6·95	*v*	1 \	1 \	6·90	.	1 /	1 /	6·20		*v*	½/
21	6·60		—		6·90	9½/	9½/	.	7·80	5½/	5 /	3 /	7·60	1 \	*v*	.	7·10	.	2½/	4 /	6·82		1½/	
22	6·85		11 /		7·40		7 /		8·30		3 /		7·95	.	.	.	7·50		6 /		7·05		5 /	
23	7·25		8½/		7·55		.		8·40		.		7·98		3 /		7·85		6 /		7·20		.	
24	7·35		4 /		7·62		3½/		8·50		.		8·02		.		8·00		.		7·26		3 /	
25	7·60		3 /		7·80		2½/		8·60		4 /		8·05		4 /		8·10		2½/		7·30		*v*	
26	7·70		*v*		7·90		*v*		8·70		*v*		8·15		3 /		8·25		.		7·48		2 \	
27	8·10		4 \		8·30		2 \		8·95		2½\		8·25		*v*		8·40	.	.	1½/	7·74		4 \	
28	8·75		7 \		8·40		2 \		9·05	3½\	3½\	3 \	8·45		2 \		8·60	.	.	2½\	7·90		6 \	8½\
29	9·05		5½\		9·00	3 \	4½\		9·65		2½\		8·75		2½\		8·82	4 \	.	.	8·42		6 \	
30	9·30		5 \		9·50		3½\		10·15		*v*		8·95		2½\		9·10	.	5½\	.	8·68		5 \	
31	9·40	3 \	2 \	2 \	9·70	1 \	*v*	2 /	10·25	1 /	4 /	4½/	9·10		*v*		9·20	.	1 \	1½/	8·80		4 \	*v*
32	9·95	2 \	*v*	2 /	10·20	2½/	3 /	3 /	10·90	5 /	6 /	6½/	9·65		8 /		9·65	.	4 /	6 /	9·20		3 /	7 /
33	10·45	3½/	6½/	8½/	10·70	6 /	9 /	11/	11·55	8 /	12 /	14 /	10·25		12½/		10·15	.	13 /	16 /	9·65		13 /	13½/
34	11·10	11½/	15 /	.	11·45	11 /	12 /	11/	12·40	.	12 /	9 /	11·05		14 /	11 /	10·90	.	17 /	12½/	10·50		16 /	15 /
35	11·75	14 /	9½/	.	12·00	.	7 /	5 /	13·00	8 /	4 /	2½/	11·70		9½/		11·50	.	9 /	6 /	11·04		10 /	3½/
36	12·25	4½/	3 /	.	12·70		*v*	2 \	13·65		*v*		11·95		*v*		12·10	.	3 /	2 /	11·60	.	*v*	5½\
37	12·60	.	.	.	13·00		.		13·95		.		12·26		2 \		12·52	.	.	.	12·10	.	7 \	.
38	12·64	.	*v*	.	13·08		3 \		13·98		2 \		12·34	.	.	.	12·68	.	3 \	.	12·28	10\	.	.
39	12·67	.	.	.	13·16		.		14·01		.		12·40	9 \	.	.	12·71	.	.	.	12·32		.	
40	12·70	.	7 \	.	13·25		8 \		14·05		6 \		12·45	.	9½\	.	12·79	.	8 \	.	12·40		14½\	

41	12·90		3½\		13·30		8½\		14·10	.	.	.	12·55		.		12·90	.	10½\	.	12·46		.	
42	13·00		3½\		13·40		12 \		14·20	.	12½\	.	12·65	.	9½\	.	13·00	.	14 \	.	12·53		16 \	
43	13·15		3 \		13·50		12 \		14·35	.	.	.	12·75		12 \		13·20	.	13 \	.	12·60	.	14 \	
44	13·40		6½\		13·70		12½\		14·50	.	13½\	.	12·90		.		13·36	.	12 \	.	12·85		11½\	
45	13·55		8 \		13·90		12½\		14·55	.	16 \	.	13·00		6½\		13·60	.	9 \	.	13·15		10 \	
46	13·75		7½\		14·00		14 \		14·60	.	.	.	13·10		4½\		13·70	.	5 \	2½\	13·28		.	
47	14·05	6½\	5 \	2½\	14·20	12½\	8 \	.	14·70	.	.	.	13·50		1½\		14·20	.	.		13·36		8 \	
48	14·55	.	1 \	v	14·70	3 \	3 \	.	14·90	.	10 \	.	13·60		.		14·30	.	½\	2 /	13·82		8 \	6 \
49	14·95	.	v	.	15·05		v		15·10	.	5 \	.	13·85		v		14·60	.	2 /	.	14·00		3½\	v
50	15·15	2 /	3 /	3½/	15·15		v		15·30	v	4½/	.	14·00	4 /	.	8 /	14·80	.	6 /	6 /	14·43	v	5 /	6 /
51	15·95		4½/		15·30		3 /		15·60	.	10 /	.	14·55		11 /		15·35		10½/	12 /	15·20		9 /	
52	16·25		8 /		16·15		8½/		15·85		17 /		14·90		9 /		15·70		11½/	11½/	15·48		7 /	
53	16·45		10 /		16·55		15 /		16·05		18 /		15·20		4 /		15·95		9 /	6 /	15·70		2 /	
54	16·75		16½/		16·85		17 /		16·40		7 /		15·80		2½/		16·40		.	3 /	15·95		2 \	
55	17·05		13½/		17·20		11½/		16·75		3 /		16·20		v		16·70		1 /		16·05		4½\	
56	17·15		6 /		17·35		7½/		17·05		v		16·35		.		16·80		.		16·18		.	
57	17·30		v		17·50		3½/		17·25		2 \		16·50		3½\		16·95		2½\		16·28		7 \	
58	17·40		2 \		17·95		v		17·45		4 \		16·65		4 \		17·10		.		16·36		9 \	
59	17·60		3½\		18·05		2 \		17·55		.		16·80		.		17·20		.		16·46		.	
60	17·80		6 \		18·20		5½\		17·65		7 \		16·90		7 \		17·25		6½\		16·56		11½\	
61	17·86		.		.		.		.		.		.		.		.		.		.		.	
62	17·92		10 \		.		.		.		.		.		.		.		.		.		.	
63	17·98		.		.		.		.		.		.		.		.		.		.		.	
64	18·04		.		.		.		.		.		.		.		.		.		.		.	
65	18·10		14½\		18·50		13½\		18·05		12½\		17·45		8 \		17·70		8 \		17·00		10 \	
66	18·15		.		.		.		.		.		.		.		.		.		.		.	
67	18·20		.		.		.		.		.		.		.		.		.		.		.	
68	18·25		11 \		.		.		.		.		.		4 \		.		2½\		.		9	
69	18·30		.		.		.		.		.		.		.		.		.		.		.	
70	18·35		6 \		18·90		17 \		18·60		8 \		17·95		3 \		18·15		v		17·50		3	
71	18·42		.		.		.		.		.		.		.		.		.		.		.	
72	18·49		4½\		.		.		.		.		.		.		.		.		.		.	
73	18·56		.		.		.		.		.		.		v		.		.		.		4½	
74	18·63		.		.		.		.		.		.		.		.		.		.		.	
75	18·70		2½\		19·40		9½\		19·15		3½\		18·50		3½/		18·65		6 /		17·95		5½	
76	18·79		.		.		.		.		.		.		.		.		.		.		.	
77	18·88		.		.		.		.		.		.		.		.		.		.		.	
78	18·97		v		.		.		.		.		.		.		.		9 /		.		.	
79	19·04		.		.		.		.		.		.		.		.		.		.		.	
80	19·15		2 /		19·95		2½\		19·70		v		19·20		7½/		19·10		12 /		18·40		10½	
End	19·80	.	5 /	7½	20·45	2 /	2½	.	20·70	.	v	v	19·70	.	.	10	19·55	.	.	13½	18·80	.	.	12½

Table I (*continued*).

No. of ring	B 2				B 3				C				C 4		D		D 3	
Centre	0 cms.				0 cms.				0 cms.				0 cms.		0 cms.		0 cms.	.
– 1	.				.				.				—	.	.		.	
2	.				.				.				—	.	.		.	
3	.				.				.				·65	.	.		.	
4	.				1·15		.		.				·75	.	.		.	
5	.				1·75		2 /		.				1·00	2 /	.		.	
6	.				1·95		*v*		.				1·15	4½/	.		.	
7	.				2·15		2 \		1·60		.		1·30	4 /	.		.	
8	.				2·40		2½\		1·85		.		1·40	2 /	.		.	
9	.				2·55	.	3 \	.	2·00		*v*		1·60	6 /	.	4 /	.	
10	.				3·00	3 \	3½\	.	2·45		*v*		2·00	4 /	1·90	2½/	.	
11	.				3·55		7 \		3·10		*v*		2·10	*v*	2·10	2½/	.	.
12	.				3·68		3½\		3·30		*v*		2·30	3 \	2·80	2½\	.	.
13	.				3·80		2½\		3·45		1 /		2·50	2 \	3·20	1 \	.	.
14	.				3·95		*v*		3·60		3 /		2·70	1 \	3·55	1 /	3·90	4 /
15	.				4·08		3 /		3·70		5 /		2·85	*v*	3·80	*v*	4·40	*v*
16	.				4·20	.	2 /		4·00		3 /		3·00	*v*	3·95	1 \	4·60	2 \
17	.				4·60	*v*	3½\	.	4·30		*v*		3·25	*v*	4·20	1 /	4·90	3 /
18	.				5·18	4½\	7½\	.	4·50		*v*		3·50	8 /	4·40	5 /	5·25	1½\
19	.	.	.	5½\	5·80	5½\	5 \	.	4·75		3 /		3·75	10 /	4·75	7½/	5·95	5 /
20	6·50	.	3 \	*v*	6·30	.	1 \	*v*	4·90		3½/		4·00	13 /	5·10	9 /	6·50	8 /
21	7·10		2½/	3½/	6·90	2½/	2½/	2½/	5·30		6½/		4·25	10 /	5·45	10½/	7·00	10 /
22	7·45		.		7·28		2½/		5·50		6 /		4·50	10 /	5·80	.	7·25	12 /
23	7·52		4 /		7·35		.		5·56		.		4·56	.	5·85	.	7·30	13 /
24	7·62		.		7·42	3½/	.	.	5·62		.		4·62	.	5·90	8½/	7·35	9½/
25	7·70		*v*		7·48		*v*		5·69		13 /		4·68	3 /	5·95	—	7·40	.
26	7·77		3½\		7·54	2 \	2 \	.	5·75		*v*		4·75	*v*	6·00	8½/	7·45	.
27	8·20		4 \		7·96		4 \		6·20		3 \		5·10	2 \	6·20	*v*	7·52	9½/
28	8·35		7 \		8·13	5½\	5½\	4½\	6·30		2½\		5·20	4 \	6·30	*v*	7·60	*v*
29	8·80		5½\		8·60		3 \		6·70		*v*		5·60	6½\	6·50	5 \	7·90	3 \
30	9·09		4 \		8·90		*v*		7·05		*v*		5·80	5½\	6·65	5 \	8·20	6 \
31	9·16		*v*		9·00		4½/		7·15		5 /		5·90	*v*	6·70	6 \	8·30	8 \
32	9·60		4 /	6½/	9·50		5 /		7·55		7½/		6·20	5½/	6·95	*v*	8·60	3½\
33	10·00	9 /	12½/	.	9·90	8½/	10 /	10/	7·95	—	14 /	14/	6·60	13 /	7·30	6 /	8·95	*v*
34	10·90	16 /	15 /	.	10·85	11½/	8 /	5½/	8·60	10½/	9½/	—	7·10	12½/	7·80	9½/	9·50	7½/
35	11·50	11 /	5 /	.	11·60	4 /	2 /	*v*	9·20		4 /		7·45	9 /	8·15	11 /	9·85	4½/
36	12·15	1½\	3½\	5 \	12·25	2 \	4 \	4 \	9·80		2½\		7·75	4 /	8·25	.	10·20	*v*
37	12·62		6 \		12·75		13 \		10·20		7½\		7·90	.	8·30	5½/	10·50	3 \
38	12·70		.		12·85		.		10·25		—		7·95	*v*	8·38	.	10·58	—
39	12·80		.		12·95		12 \		10·30		—		8·00	.	8·46	*v*	10·66	5 \
40	12·85		12½\		13·05		14½\		10·35		12 \		8·05	5 \	8·55	5 \	10·75	7 \

41	12·95		.		13·20		16 \		10·45	.	8·10	.	8·65	.	10·80	.
42	13·08		16 \		13·30		16 \		10·55	14½\	8·20	.	8·70	.	10·85	14 \
43	13·20		16 \		13·45		14½\		10·70	.	8·25	9 \	8·80	.	10·90	.
44	13·45		12½\		13·65		12 \		10·80	.	8·40	.	8·90	10 \	11·00	.
45	13·70		7 \		13·90		10 \		10·85	15½\	8·50	11 \	9·05	.	11·10	6 \
46	13·90		6 \		14·05		5½\		10·90	.	8·55	.	9·25	.	11·20	3 \
47	14·05		4 \		14·15		1 \		11·05	10½\	8·65	3 \	9·30	4 \	11·50	v
48	14·45		2 \		14·55	v	2 /	.	11·25	.	8·85	v	9·70	v	11·60	3 /
49	14·85		v		14·90	.	2 /	.	11·42	v	9·00	6 /	10·00	3½	11·85	6 /
50	15·00	v	2½/	3 /	15·05	3 /	4 /	.	11·50	5 /	9·15	9 /	10·15	6 /	12·00	9 /
51	15·55		6 /		15·60		4 /		12·05	11 /	9·65	14 /	10·65	.	12·50	9 /
52	15·90		7½/		15·95		6 /		12·45	15½/	9·85	12½/	11·00	2 /	13·00	2 /
53	16·15		10½/		16·20		9 /		12·80	12 /	10·20	6½/	11·40	4 \	13·40	1 \
54	16·38		5½/		16·43		5 /		13·00	9½/	10·80	v	11·85	.	13·85	3 \
55	16·48		2 \		16·58		v		13·30	2½/	11·15	4 \	12·25	.	14·10	4 \
56	16·55		5 \		16·68		3 \		13·55	v	11·35	6½\	12·40	.	14·25	6 \
57	16·65		6½\		16·80		5 \		13·70	2 \	11·60	8 \	12·50	.	14·40	8 \
58	16·78		—		16·90		6 \		14·25	6 \	11·80	11 \	12·70	13 \	14·60	10 \
59	16·84	6½\	—		16·98		.		14·35	.	12·00	13 \	12·85	.	14·70	.
60	16·90	.	11 \	.	17·08		10 \		14·45	8 \	12·15	12 \	12·95	18½\	14·80	12 \
61	.		.		.		.		.	.	.	.	.	.	.	.
62	.		.		.		13 \		.	.	.	.	.	.	.	4½
63	.		.		.		.		.	.	.	.	.	.	.	.
64	.		.		.		.		.	.	.	.	.	.	.	.
65	17·30		8½\		17·43		8½\		14·95	6 \	12·90	9 \	13·50	12½\	15·15	11½\
66	.		.		.		.		.	.	.	.	.	.	.	.
67	.		.		.		.		.	.	.	.	.	.	.	.
68	.		6 \		.		.		.	.	.	.	.	.	.	.
69	.		.		.		.		.	.	.	.	.	.	.	.
70	17·68		4 \		17·65		4 \		15·35	4 /	13·55	v	13·85	5 \	15·40	4½
71	.		.		.		.		.	.	.	.	.	.	.	.
72	.		.		.		2 \		.	.	.	.	.	.	.	.
73	.		v		.		.		.	.	.	.	.	.	.	.
74	.		.		.		.		.	.	.	.	.	.	.	.
75	18·10		4 /		18·00		2½/		15·80	6½	.	5½	14·30	4½/	15·60	4 /
76	.		.		.		.		.	.	.	.	.	.	.	.
77	.		5½/		.		5 /		.	.	.	.	.	.	.	.
78	.		.		.		.		.	.	.	.	.	.	.	.
79	.		.		.		.		.	.	.	.	.	.	.	.
80	18·58		9 /		18·38		5 /		16·00	9 /	14·55	8	14·60	1½/	15·85	6 /
End	18·90	.	.	5 /	18·75	.	.	3 /	16·50	6 /	15·15	3 /	15·10	v	16·30	3 /

Table II. *Shorea robusta.* Longitudinal series.

The first column of each stick gives distance of each ring in centimetres from the centre, and the second column inclinations of the grain in degrees in the different rings. Where the rings were broad three readings could be taken, at the beginning, middle and end of the ring. Straight grain denoted by “*v*,” right-handed inclination by “/” and left-handed inclination by “\.”

No. of ring	No. 1		No. 2		No. 3		No. 4		No. 5		No. 6	
	cms.		cms.		cms.		cms.		cms.		cms.	
10	0	. .	1·60	4½\ 6\ .	1·60	3\ 4½\ .	1·40	*v* 1½\ .	1·30	*v* *v* .	1·20	*v* 4\
11	.	6\ 7½\	.	5\	.	3\	.	2\	.	3½\	.	2\
12	.	4\	.	1\	.	1\	.	2½\	.	*v*	.	*v*
13	.	2½\	.	*v*	.	*v*	.	2½\	.	*v*	.	1\
14	.	1\	.	*v*	.	*v*	.	1½\	.	2½\	.	3\
15	1·75	4½\ 2½\ 2\	3·00	1\	3·00	*v*	2·90	*v*	2·80	2½\	2·70	3\
16	.	3\	.	*v*	.	1/	.	1\	.	2½\	.	3\
17	.	1/	.	1/	.	1½\	.	2\	.	1\	.	*v*
18	.	2/	.	*v*	.	1½\	.	*v*	.	*v*	.	2/
19	.	*v*	.	4\	.	4\	.	*v*	.	2½\	.	5½/
20	4·40	4½\	5·50		5·50		5·30		5·20		5·20	
21	.	7\	.	6½\	.	4\	.	3\	.	*v*	.	*v*
22	.	3½\	.	*v*	.	2½/	.	3/	.	2/	.	3\
23	.	*v*	.	6½/	.	6/	.	3½/	.	*v*	.	4\
24	.	4/	.	7½/	.	6/	.	2½/	.	4½\	.	9\
25	6·45	. 6/ .	7·60	7½/	7·60	6½/	7·60	3/	7·60	*v*	7·70	3½\
26	.	8/	.	5½/	.	2/	.	3\	.	2/	.	*v*
27	.	*v*	.	1½\	.	4½\	.	7\	.	4\	.	3½\
28	.	4½\	.	7\	.	7½\	.	9½\	.	8\	.	6\
29	.	10½\	.	12\	.	10\	.	14\	.	12\	.	13\
30	8·90	17\	10·10	17½\	10·10	15½\	10·00	18\	10·00	15\	10·00	12½\
31	.	.	.	.	.	.	.	.	.	.	.	.
32	.	.	.	.	.	.	.	.	.	.	.	.
33	.	10½\	.	12\	.	13\	.	14½\	.	12\	.	11\
34	.	.	.	5½\	.	6\	.	.	.	8½\	.	7\
35	9·65	3\	10·80	*v*	10·80	1½\	10·60	3\	10·60	2\	10·60	*v*
36	.	3½/	.	3/	.	*v*	.	*v*	.	*v*	.	2½/
37	.	4/	.	1½/	.	1½/	.	*v*	.	1/	.	3½/
38	.	4½/	.	7/	.	7/	.	7/	.	8/	.	7/
39	.	10/	.	12/	.	9½/	.	9/	.	10/	.	9/
40	10·70	9½/	11·90	12½/	11·90	13/	11·70	12½/	11·70	13/	11·70	12/

41	.	5½/	.	5½/	.	6 /	.	6 /	.	5½/	.	7 /
42	.	1½\	.	1 \	.	v	.	v	.	2 \	.	1 \
43	.	5 \	.	4 \	.	5 \	.	7 \	.	5 \	.	5 \
44	.	v	.	2½\	.	v	.	2 \	.	1 \	.	3 \
45	12·90	3 /	14·20	6 /	14·20	4½/	14·10	v	14·10	v	14·10	v
46	.	.	.	.	.	.	.	.	.	.	.	.
47	.	12 /	.	10 /	.	7½/	.	.	.	2 /	.	6 /
48	.	.	.	.	.	.	.	2½/	.	.	.	.
49	.	.	.	.	.	.	.	.	.	.	.	.
50	13·35	10 /	14·60	10½/	14·60	10 /	14·50	6½/	14·60	6 /	14·50	7 /
51	.	4½/	.	.	.	.	.	.	.	.	.	.
52	.	3½/	.	5½/	.	3 /	.	v	.	v	.	v
53	.	.	.	2½/	.	v	.	.	.	3 \	.	2 \
54	.	.	.	.	.	1 \	.	.	.	3½\	.	5½\
55	14·15	3½\	.	4 \	.	7½\	.	9 \	.	7 \	.	7 \
56	.	.	.	.	.	.	.	.	.	.	.	.
57	.	.	.	7 \	.	10 \	.	10½\	.	8½\	.	9 \
58	.	8½\	.	.	.	.	.	.	.	.	.	.
59	.	.	.	.	.	.	.	.	.	.	.	.
60	14·80	12 \	16·00	12 \	16·00	12½\	15·90	13 \	15·90	13 \	15·90	13 \
65		13 \	.	13 \	.	15½\	.	17½\		14½\		15 \
End	.	. . 14\	16·70	. 13 \	16·70	17½\	16·60	20 \	16·60	19 \	16·60	16½\

Table II (*continued*).

No. of ring	No. 7			No. 8			No. 9			No. 10			No. 11			No. 12		
	cms.			cms.			cms.			cms.			cms.			cms.		
10	1·30	*v*	*v*	1·20	2 /	1 /	1·10	4½/	*v*	1·30	3/	2 /	1·50	2/	1 /	1·30	*v*	2 /
11	.		1 /	.		*v*	.		1 \	.		1 \	.		2 \	.		1 \
12	.		2½/	.		1 \	.		2½\	.		3 \	.		3 \	.		2 \
13	.		2 \	.		2 \	.		3½\	.		2½\	.		3 \	.		1½\
14	.		2½\	.		3½\	.		3½\	.		2½\	.		3½\	.		4 \
15	2·70		4 \	2·70		3 \	2·70		2½\	2·70		2½\	2·80		1 \	2·70		2½\
16	.		*v*	.		*v*	.		*v*	.		*v*	.		2 /	.		1 /
17	.		2 /	.		3½/	.		3 /	.		3 /	.		4 /	.		3½/
18	.		5 /	.		4 /	.		3½/	.		3½/	.		6 /	.		8 /
19	.		7½/	.		5 /	.		*v*	.		3 /	.		7 /	.		5½/
20	5·10			5·00			5·00			5·00			5·00			5·00		
21	.		*v*	.		4 \	.		8 \	.		3 \	.		*v*	.		2 /
22	.		8 \	.		8½\	.		6 \	.		6 \	.		7 \	.		3½\
23	.		8½\	.		7 \	.		7 \	.		9½\	.		8 \	.		7 \
24	.		5 \	.		2 \	.		4 \	.		2½\	.		2½\	.		3½\
25	7·75		*v*	7·60		*v*	7·60		*v*	7·60		*v*	7·70		3½/	7·70		2½/
26	.		5 /	.		7 /	.		7 /	.		9 /	.		10 /	.		7 /
27	.		*v*	.		5 /	.		7 /	.		5 /	.		7½/	.		6 /
28	.		2 \	.		2 \	.		2½\	.		*v*	.		*v*	.		2 /
29	.		9½\	.		7 \	.		8 \	.		4 \	.		4½\	.		4 \
30	10·00		11½\	10·00		9½\	10·00		9 \	10·10		11 \	10·20		10 \	10·10		7 \
31	.		.	.		.	.		.	.		.	.		.	.		.
32	.		.	.		.	.		.	.		.	.		.	.		.
33	.		9 \	.		6 \	.		9 \	.		9 \	.		9½\	.		11 \
34	.		2½\	.		5 \	.		7 \	.		5½\	.		7 \	.		7 \
35	10·60		*v*	10·60		*v*	10·60		*v*	10·70		2 \	10·80		2½\	10·70		4 \
36	.		2½/	.		2 /	.		*v*	.		*v*	.		*v*	.		2 \
37	.		7 /	.		6 /	.		.	.		.	.		.	.		.
38	.		8½/	.		9½/	.		6 /	.		7 /	.		6½/	.		3½/
39	.		11 /	.		12 /	.		11 /	.		9 /	.		10 /	.		8½/
40	11·70		16 /	11·70		14 /	11·60		12½/	11·70		13 /	11·80		14½/	11·70		13½/

41	.	5½/	.	7 /	.	6½/	.	7½/	.	7 /	.	6½/
42	.	2 /	.	2 /	.	*v*	.	*v*	.	1 /	.	*v*
43	.	4 \	.	4½\	.	5 \	.	3 \	.	4½\	.	3½\
44	.	2½\	.	7 \	.	10 \	.	7½\	.	9½\	.	8 \
45	14·00	*v*	14·10	1½\	14·00	7 \	14·10	10 \	14·20	10½\	14·10	10 \
46	.	.	.	.	.	.	.	.	.	.	.	.
47	.	3 /	.	2 /	.	*v*	.	5 \	.	7½\	.	9 \
48	.	.	.	.	.	.	.	.	.	.	.	.
49	.	.	.	.	.	.	.	.	.	.	.	.
50	14·50	5½/	14·50	5 /	14·50	3 /	14·50	*v*	14·60	2 \	14·50	3½\
51	.	.	.	.	.	.	.	.	.	.	.	.
52	.	*v*	.	*v*	.	*v*	.	2½\	.	4 \	.	*v*
53	.	.	.	*v*	.	1½\	.	4 \	.	4½\	.	3 \
54	.	.	.	3½\	.	.	.	.	.	.	.	.
55	.	6½\	.	7 \	.	7½\	.	8½\	.	8 \	.	9½\
56	.	.	.	.	.	.	.	.	.	.	.	.
57	.	9 \	.	10 \	.	12 \	.	10½\	.	10 \	.	10½\
58	.	.	.	.	.	.	.	.	.	.	.	.
59	.	.	.	.	.	.	.	.	.	.	.	.
60	15·90	12 \	15·90	12 \	15·80	14½\	15·80	13 \	15·90	13½\	15·80	13 \
65	.	13½\	.	14 \	.	17 \	.	15 \	.	16½\	.	15 \
End	16·50	17½\	16·50	16 \	16·40	18½\	16·40	18½\	16·50	18½\	16·40	20 \

Table II (*continued*).

No. of ring	No. 13			No. 14			No. 15			No. 16			No. 18		
	cms.			cms.			cms.			cms.			cms.		
10	1·20	*v*	3 /	1·10	3/	3½/	1·10	2/	4 /	1·00	*v*	4½/	·45	4/	2 /
11	.		*v*	.		2 /	.		3 /	.		1½/	·70		*v*
12	.		1 \	.		*v*	.		1 \	.		1½\	1·05		2 \
13	.		2½\	.		3½\	.		3 \	.		2½\	1·30		4 \
14	.		3½\	.		5½\	.		3½\	.		4½\	1·70		1 \
15	2·60		3 \	2·60		3 \	2·50		1½\	2·40		2½\	2·10		*v*
16	.		1 \	.		*v*	.		1½/	.		3 /	2·60		4 /
17	.		2½/	.		3 /	.		5 /	.		4 /	3·10		4
18	.		7½/	.		8½/	.		8 /	.		7 /	3·70		8½
19	.		5 /	.		6 /	.		6½/	.		6 /	4·20		5½/
20	5·00			5·00			5·00			5·00					
21	.		3½/	.		1½/	.		1½/	.		*v*	4·50		*v*
22	.		3½\	.		3½\	.		4½\	.		6 \	5·10		6 \
23	.		8 \	.		7 \	.		8 \	.		7½\	5·75		8½\
24	.		4 \	.		3 \	.		5½\	.		4 \	6·25		2½\
25	7·70		*v*	7·60		2 /	7·60		*v*	7·50		3 /	7·00		3½/
26	.		7½/	.		7 /	.		5 /	.		6 /	7·40		9 /
27	.		6 /	.		7 /	.		6 /	.		6 /	8·05		7 /
28	.		2 /	.		3 /	.		1 /	.		2½/	8·70		3 /
29	.		4½\	.		2½\	.		4½\	.		3 \	9·30		2½\
30	10·10		9 \	10·10		5 \	10·10		7 \	10·10		9 \	9·75		5½\
31	.		.	.		.	.		.	.		.	9·80		.
32	.		.	.		.	.		.	.		.	9·90		.
33	.		13½\	.		10½\	.		9½\	.		11½\	10·00		11 \
34	.		9 \	.		7 \	.		7½\	.		7½\	10·10		.
35	10·70		6½\	10·60		4 \	10·70		4 \	10·60		6 \	10·20		4½\
36	.		3 \	.		1½\	.		2 \	.		4½\	10·40		3½\
37	.		.	.		.	.		.	.		.	10·50		*v*
38	.		2½/	.		4 /	.		2½/	.		1½/	10·60		3 /
39	.		6 /	.		8 /	.		6 /	.		6½/	10·90		4 /
40	11·70		11 /	11·60		12 /	11·70		10½/	11·60		10 /	11·20		9 /

41	.	5 /	.	6 /	.	4 /	.	4 /	11·80	3 /
42	.	1 /	.	r	.	v	.	r	12·50	v
43	.	4½\	.	3½\	.	4 \	.	4 \	13·00	5 \
44	.	7½\	.	12 \	.	7½\	.	8 \	13·45	9 \
45	14·10	13 \	14·00	12 \	14·10	11 \	14·00	12½\	13·70	13 \
46	.	.	.	.	.	.	.	.	13·80	.
47	.	9 \	.	9 \	.	11½\	.	12 \	13·90	17 \
48	.	.	.	.	.	.	.	.	14·00	.
49	.	.	.	.	.	.	.	.	14·10	.
50	14·50	4 \	14·50	3½\	14·60	7 \	14·50	9½\	14·20	13 \
51	.	.	.	.	.	.	.	.	.	.
52	.	r	.	r	.	2 \	.	6 \	.	.
53	.	1 \	.	1 /	.	1 \	.	3 \	.	9 \
54	.	.	.	.	.	.	.	.	.	.
55	.	8 \	.	4 \	.	r	.	2 \	14·70	5 \
56	.	.	.	.	.	.	.	.	.	.
57	.	.	.	6 \	.	6 \	.	4 \	.	1 \
58	.	10½\	.	.	.	.	.	.	.	.
59	.	.	.	.	.	.	.	.	.	.
60	15·70	12½\	15·70	9½\	15·80	8 \	15·70	7½\	15·10	r
65	.	17½\	.	12 \	.	12½\	.	10½\	.	.
End	16·30	19 \	16·30	17 \	16·40	14½\	16·30	13 \	15·75	6 \

causes, first, the numbering of the rings was done without comparison between the two series, and secondly, the fainter rings did not stand out so clearly in the sticks of the longitudinal series, with the result that a certain number of them escaped observation. However, the spacing of the rings and the phase of inclination shown by the grain clearly indicate that the 30th to 60th ring inclusive of the transverse series correspond with those numbered from 24 tô 50 in the longitudinal series.

The diagram illustrating the longitudinal series (Fig. 4) shows that the curves which indicate the course of the grain in each stick agree together very closely as to form, a fact foreshadowed by the longitudinal parallel zones to be seen on the surface of a radial board, and demonstrate that in a radial plane the inclination of the grain alternates between left-handed and right-handed with the growth of the tree.

On reading off from Fig. 4 the position of each maximum inclination of the grain with reference to the rings, for the successive sticks of the longitudinal series it is seen that the position of each corresponding maximum inclination may remain the same through the series, for example, the one occurring between the 40th and 41st rings, or else it may vary within a range of two or three rings, or finally, as in the last two periods, the position of a maximum inclination of the grain may pass, on being traced through successive transverse levels, more to the exterior or *vice versa*, according to whether the series is examined from the one end or the other.

Thus in *Shorea robusta* it is apparent that though the periods are structurally continuous, their development at different transverse levels in the same radial plane is not necessarily simultaneous, though it usually is so.

From the curves for sticks 1 to 9 (Fig. 4) it is seen that some of the earlier periods do not retain their identity throughout the series; the period comprised between the 12th and 20th rings in stick 6 fades away in sticks 5 to 1, its place being taken by a fresh period. The board, unfortunately, was not long enough to extend beyond this transitional region to where the new period would be fully established.

In some of the other species this fading away of some periods and the increase in the prominence of others was of much more frequent occurrence, and constituted one of the chief causes of lack of correspondence shown by successive curves of a series whether transverse or longitudinal.

That the appearance of this transitional region is not due to errors in the determination of the inclination of the grain is proved by the

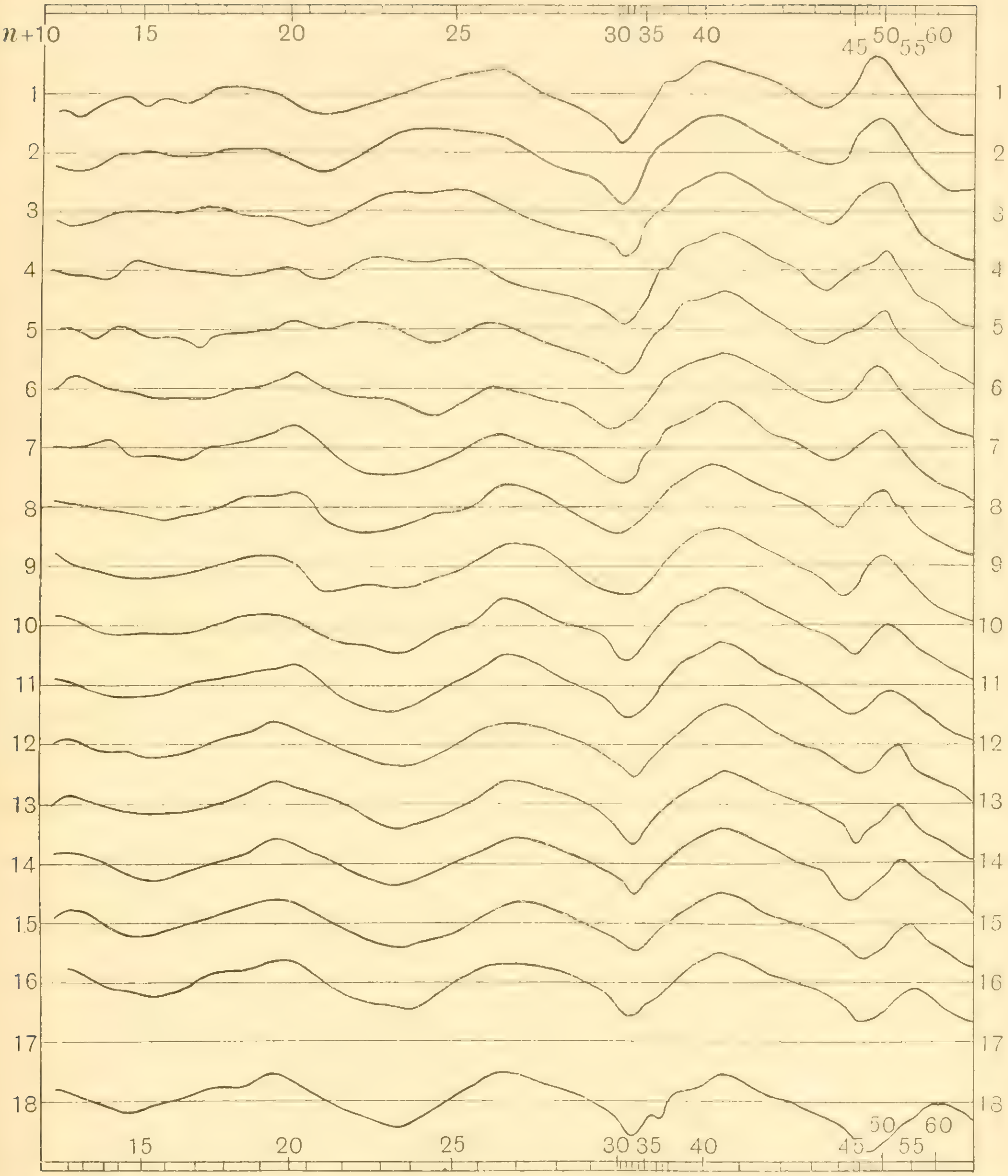


Fig. 4. *Shorea robusta.* Longitudinal series. A series of curves showing inclination of the grain along successive transverse sticks from a radial board an inch apart. Scale as in Fig. 3.

forms of the series of fractures obtained by the radial fracture of a series of sticks sawn transversely from the radial board adjacent to the one which supplied the data for the longitudinal series of curves (photograph 1).

It has already been pointed out that in a radial plane the positions of the periods are not rigidly fixed with reference to the growth-rings, and that there may be a considerable interval between the different transverse levels as to the time of the inception of a period. There is still a further inconstancy discoverable in the series. The actual inclination of the grain at different transverse levels in the same radial plane is not uniform at any ring, but varies in a very indefined manner from stick to stick, and coupled with this is a corresponding variation in the rate of change in the inclination of the grain.

The following example will serve to illustrate these variations. Between the 40th and 41st rings, Fig. 4, there is a maximum right-handed phase in all the sticks of the longitudinal series. Now the inclination of the grain at this point varies in a very irregular manner between 0 and 16 degrees, a range of variation far in excess of the probable error in measurement which was estimated at one degree.

Between the 42nd and 43rd ring the grain has become vertical, hence the rate of change in inclination of the grain could not have been uniform at the different transverse levels.

From the 43rd ring onwards the direction of the change in the inclination of the grain is still the same and reaches a maximum left-handed inclination of five degrees between the 43rd and 44th rings at the level of stick 1, after which the change in inclination of the grain becomes right-handed.

At other transverse levels, however, the grain is becoming still more left-handed, reaching a maximum of 13 degrees at the 45th ring in the 13th stick and of 17 degrees at the 48th ring of the 18th stick.

If the periodic changes in the inclination of the grain were simultaneous with periods of growth and the amplitude of the periods was constant, the grain would consist of a series of alternate left-handed and right-handed spirals (double spiral grain), but on account of the irregularities described above, the grain is composed of a series of superposed serpentine curves grading one into the other which, for short lengths of the trunk at least, tend to be arranged in the form of a double spiral.

The transverse series of curves (Fig. 3) shows a complete parallel correspondence in all points with the longitudinal series. At a transverse level the periodic changes in the inclination of the grain are continuous tangentially, the periods are not rigidly fixed with reference to the growth-rings, or in other words the periods are only approximately simultaneous, and finally the inclination of the grain at corresponding phases of a period vary from stick to stick. The result is that, though the inclination of the grain alternates between left-handed and right-handed when traced ring by ring from the centre to the exterior, around no ring is the inclination of the grain uniform while often it may change several times from left-handed to right-handed on being followed round. All these points can be followed in a careful scrutiny of the transverse series of curves.

The course of the grain having been determined there still remain some points of secondary importance to be investigated, namely the relations that exist between period length, amplitude, width of rings and age to tree.

In determining average period lengths and average amplitudes all doubtful cases were neglected in transitional regions where one set of periods was vanishing and another set appearing in its place.

The radial distance between two successive maximum right-handed or left-handed inclinations was used for obtaining average period lengths rather than the distance between succeeding vertical phases, since the former was likely to give more reliable figures as it may happen that a period may remain completely right-handed or left-handed in its inclination; for example, the period between the 47th and the last ring in the 16th stick of the longitudinal series which is wholly left-handed.

In Tables III and IV are given the period lengths in centimetres for the sticks of the longitudinal and transverse series respectively, and in addition is given the average period length for each stick and also the average length of the successive periods throughout the series.

The figures in Table III show that the greatest period length (4·15 cms.) in the longitudinal series is reached by the period comprised between the 15th and 23rd rings and that subsequently a decrease in the period length sets in. Correlated with the gradual shift of the last two periods towards the exterior (see Fig. 4) the average period length at the different levels in the longitudinal series shows a gradual increase from stick 6 to stick 18 (last column, Table III).

The measurements of the period lengths of the transverse series (Table IV) demonstrates that the average period length increases with age, as in the longitudinal series, to a maximum (4·35 cms.), after which it decreases. On comparing together the average period lengths of the different sticks it is seen that the period length varies directly with the radial rate of growth. That this should be so is to be inferred from the excentric growth of the tree and the tangential continuity of the periods in a transverse plane.

Table III.

Shorea robusta. Period lengths in centimetres in the longitudinal series.

Range of period in growth-rings	10–20	15–23	20–26	23–31	26–40	31–45	40–55	Average
	cms.	cms.	cms.	cms.	cms.	cms.	cms.	cms.
6th stick	3·75	4·40	3·40	3·00	3·90	3·65	2·65	3·54
7th ,,	3·20	3·70	3·45	4·05	3·90	3·50	2·65	3·50
8th ,,	4·25	3·35	3·70	4·35	3·50	3·80	2·80	3·68
9th ,,	—	3·85	4·35	4·40	3·50	3·70	2·75	3·76
10th ,,	3·65	4·20	4·15	3·85	3·75	3·85	2·75	3·79
11th ,,	4·15	4·35	3·60	4·05	3·65	3·80	2·85	3·79
12th ,,	3·55	4·25	4·05	4·00	3·60	3·80	2·90	3·74
13th ,,	3·55	4·10	3·95	4·00	3·65	3·70	2·90	3·70
14th ,,	3·40	4·10	4·05	4·05	3·60	3·60	3·05	3·70
15th ,,	3·45	4·30	4·15	4·05	3·40	3·90	3·20	3·78
16th ,,	3·80	4·35	3·85	3·70	3·50	3·90	3·30	3·77
17th ,,	—	—	—	—	—	—	—	—
18th ,,	—	4·50	3·85	2·95	3·70	4·05	3·70	3·96
Average	3·68	4·15	3·88	3·96	3·64	3·77	2·96	3·73
No of rings per period	8	7	7	13	13	13	23	—

Table IV.

Shorea robusta. Period lengths in centimetres in the transverse series.

Range of period in growth-rings		25–35	30–44	35–53	44–63	53–end	Average
		cms.	cms.	cms.	cms.	cms.	cms.
Radial sticks from the disc	A	4·35	4·70	5·50	4·35	3·10	4·40
	A 1	4·80	4·60	5·25	4·80	3·70	4·64
	A 4	4·10	5·55	3·65	3·40	4·50	4·24
	A 7	3·05	3·90	3·85	4·50	5·00	4·06
	B	3·35	4·10	4·15	4·50	4·20	4·06
	B 1	3·57	4·11	4·58	4·30	3·45	3·99
	B 2	3·41	4·40	5·50	3·80	2·30	3·88
	B 3	3·50	5·17	5·45	4·00	2·20	4·06
	C	2·56	4·55	4·40	3·80	3·35	3·73
	D	2·40	2·20	2·45	3·40	3·70	2·83
	D 3	2·30	2·45	2·80	4·10	3·35	3·00
Average		3·40	4·15	4·35	4·10	3·55	3·90
No. of rings per period		13	15	18	20	32	—

The magnitude in degrees of the successive right-handed and left-handed swings in the inclination of the grain are given for the longitudinal and transverse series in Tables V and VI respectively. The

Table V. *Shorea robusta.* Table showing the amount in degrees of the successive right- and left-handed swings of the grain for the longitudinal series.

Change in direction of grain and the rings between which included	Left 12th–15th	Right 15th–20th	Left 20th–23rd	Right 23rd–26th	Left 26th–31st	Right 31st–40th	Left 40th–45th	Right 45th–55th	Left 55th–end	Average
1st stick	—	—	9°	15°	26°	28°	16°	17°	27°	—
2nd ,,	—	—	7	13	25	30	17	15	24	
3rd ,,	—	—	6	14	22	29	18	15	27	—
4th ,,	—	—	5	7	22	31	20	13	27	—
5th ,,	—	—	—	—	17	28	18	11	26	—
6th ,,	7°	9°	15	10	14	25	17	12	23	15°
7th ,,	7	11	16	14	17	28	20	10	25	16
8th ,,	7	9	13	16	17	23	20	12	22	15
9th ,,	11	8	12	16	17	22	23	13	22	16
10th ,,	6	7	13	18	20	24	23	10	20	16
11th ,,	6	11	15	19	21	25	25	8	16	16
12th ,,	6	12	15	15	18	25	24	10	22	16
13th ,,	6	10	16	16	22	25	24	13	20	17
14th ,,	9	15	16	16	19	22	25	14	19	17
15th ,,	8	12	16	15	16	20	22	12	17	15
16th ,,	10	13	16	14	17	21	23	11	—	16
18th ,,	8	13	18	19	21	20	26	17	—	18
Average swing	8	11	13	15	19	25	20	13	22	16

Table VI. *Shorea robusta.* Table showing the amount in degrees of the successive right- and left-handed swings of the grain for the transverse series.

	Change in direction of grain and the rings between which included	Left 25th–30th	Right 30th–35th	Left 35th–44th	Right 44th–53rd	Left 53rd–63rd	Right 63rd–80th	Average	Average period length in cms.
Radial sticks from the disc	A	19°	23°	23½°	25°	30½°	23°	24°	4·40
	A 1	13	16	26	32	35	22	24	4·64
	A 4	14	17½	30	35	31	13	25	4·24
	A 7	7	18	27	23	20	20	19	4·06
	B	11	23	31	26	21	23	23	4·06
	B 1	14	24	33	27	23	25	24	3·99
	B 2	12	23	32	26	21	20	22	3·88
	B 3	7	18	28	26	23	17	20	4·06
	C	16	18	32	32	24	18	23	3·73
	D	17	17	21	16	20	18	18	2·83
	D 3	21	16	22	24	24	20	21	3·00
Average swing		14	19	28	27	25	20	22	3·90

average (Table V) amplitude remains approximately constant at the successive transverse levels in the longitudinal series, its value ranging between 15 and 18 degrees, but on the other hand the average value of the successive swings increases with age up to a maximum of 25 degrees which is followed by a slight subsequent decrease in value. The figures of Table VI show that the same is true of the transverse series. Although both period length and amplitude reach their maximum value at about the same time, yet the two do not appear to be very closely correlated, for the subsequent decrease in the period length is so much greater than the decrease in the amplitude that the ratio of period length to amplitude steadily decreases with age except for the last period of the transverse series which shows a slight decrease.

On comparing together the average period length and the average amplitude, there are indications that in the transverse series the longer periods are correlated with bigger amplitudes, but no such correlation is apparent in the longitudinal series.

The correlation of period length and amplitude with width of ring is much more indefinite and is only recognisable in so far as all three tend to increase with age up to a maximum which is followed by a greater or smaller subsequent decrease.

CHLOROXYLON SWIETENIA.

The curves of the longitudinal and transverse series are given in Figs. 5 and 6 respectively, but the data from which they have been constructed are not printed here.

The numbering of the rings in the two series is practically identical as the several zones of narrow rings afforded reliable points for comparison.

Due to the uniformity in the rate of growth, the proportional width of the rings remained the same along the different radii of the transverse disc, so the ring widths were only measured along three of the sticks. In the longitudinal series the ring widths were fully measured along one stick from the middle of the series.

An examination of the longitudinal and transverse series of curves shows that the course of the grain in *Chloroxylon Swietenia* is very similar to what it is in *Shorea robusta.* The periodic changes in the inclination of the grain are continuous both longitudinally in a radial plane and tangentially at a transverse level. The inclination of the grain at corresponding points of a period does not remain the same in adjacent sticks of the transverse series or at the different transverse levels in the longitudinal series, a striking instance occurring at the 100th ring of the

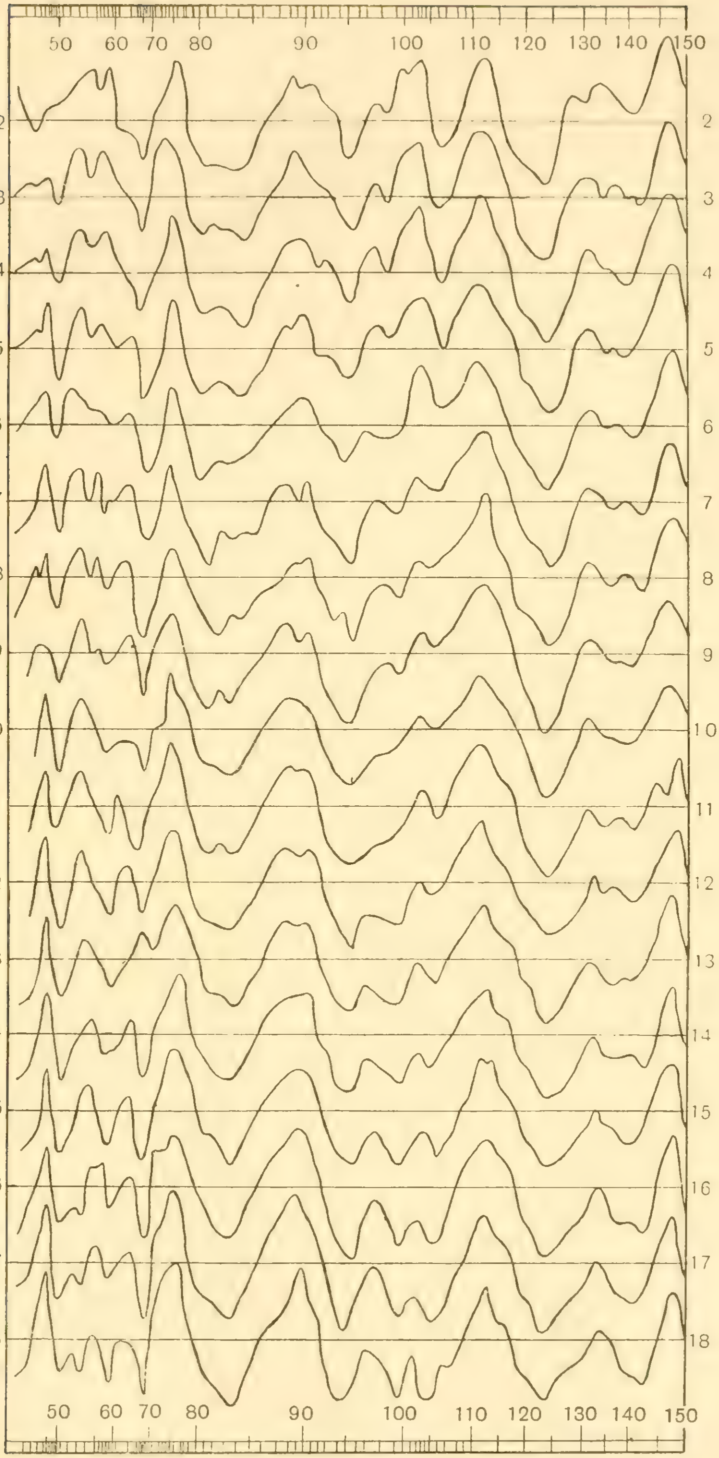


Fig. 5. *Chloroxylon Swietenia.* Longitudinal series. Scale as in Fig. 3.

longitudinal series. The consequence is that the rate of change in the inclination of the grain will not be uniform at any moment, resulting in the grain being composed of a series of superimposed serpentine curves.

Although the general course of the grain in *Chloroxylon Swietenia* and *Shorea robusta* agree very closely together, yet, as might be expected, there are numerous minor differences between the two species.

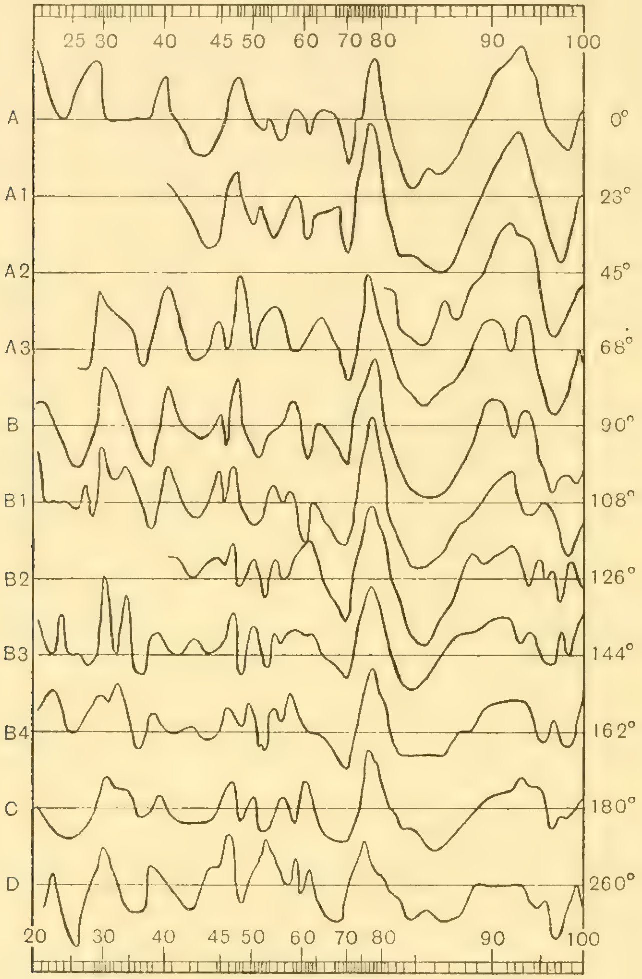


Fig. 6. *Chloroxylon Swietenia*. Transverse series. Scale as in Fig. 3.

The length of the period which in *Shorea robusta* ranges between 3 and 4 cms. has an average value of a little less than 1 cm. in *Chloroxylon*

Swietenia. The amplitude is greater in *Chloroxylon*, reaching a maximum of 40 degrees as compared with 30 degrees in *Shorea.*

The net result of a shorter period and a bigger amplitude is that the rate of change in the inclination of the grain will be more rapid, and when this is combined with narrow growth-rings errors in the practical work of investigation will be much more frequent than under the opposite conditions of broad rings and a slow rate of change in the inclination of the grain.

In spite of these disadvantages in *Chloroxylon Swietenia* the Plate, fig. II, of the series of curved fractures obtained by the method of radial splitting, shows that the errors from this source are not so serious as might be expected.

On comparing the position of the periods with reference to the growth-rings in the sticks of the two series it is seen that the periods in *Chloroxylon* are much more closely connected with the growth-rings and show no tendency to cut across periods of growth as in *Shorea robusta.*

Exceptions to this contemporaneity of the periods are due to the somewhat frequent appearance of subsidiary or union periods which retain their identity through a series for short distances only, the period appearing at the 44th ring in sticks A3, B, B1 and B2 if the transverse series is a case in point. Many more of these subsidiary periods can be recognised in the curves of the transverse and longitudinal series.

On account of the frequent appearance of these subsidiary periods it was difficult to obtain data which could be relied on to the relation between period length, amplitude, width of ring and age.

If the 15th stick of the longitudinal series is taken as representing the average condition of the grain for the series it is seen that long periods occur equally where the rings are broad as where they are narrow. No gradual increase in period length, with age, up to a maximum followed by a subsequent decrease is seen as in *Shorea robusta.*

On the other hand it was found on calculating the average that the biggest amplitudes were always correlated with the longest periods.

GMELINA ARBOREA.

The examination of *Gmelina arborea* showed that the grain possesses the same serpentine character that is characteristic of the two species already described.

The method of radial splitting as applied to a portion of the disc showed that the periods are tangentially continuous at a transverse level (see Plate, III). The series of curves which were obtained from the

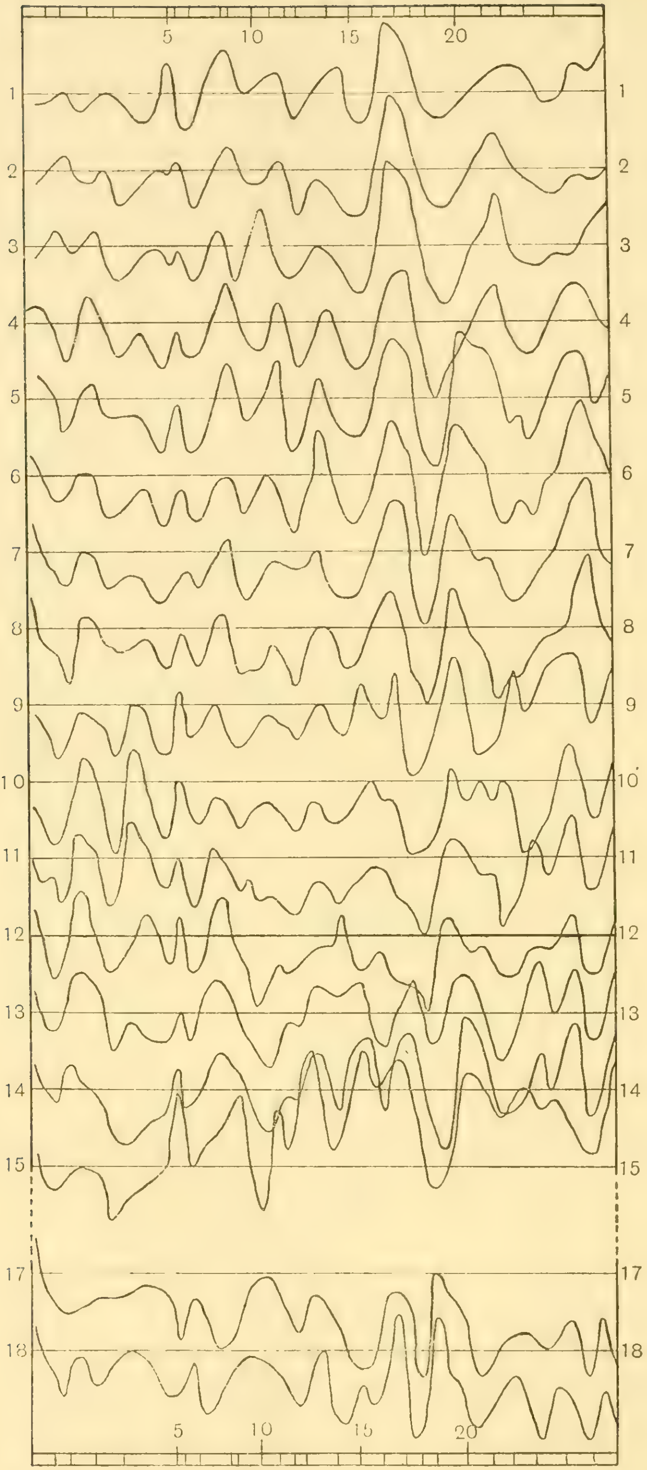


Fig. 7. *Gmelina arborea*. Longitudinal series. Same scale as Fig. 3.

examination of the sticks of the transverse series, however, showed very poor correspondence. This lack in correspondence was due to inaccuracies attributable to the great excentricity of the trunk, the short period

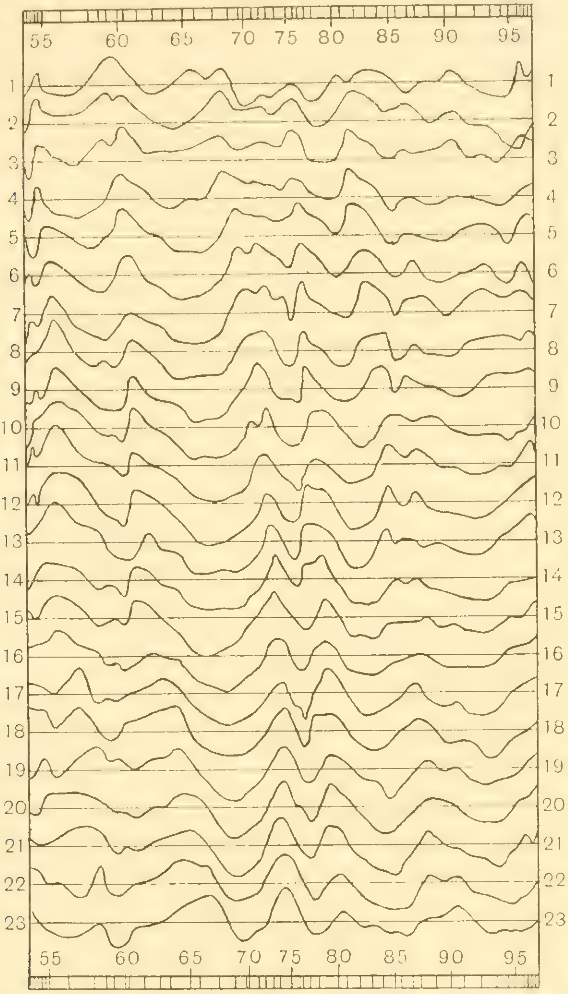


Fig. 8. *Xylia dolabriformis.* Longitudinal series. Same scale as Fig. 3.

length (0·70 cms.) and the frequency with which adjacent rings coalesced for comparatively long tangential distances.

The character of the longitudinal series of curves (Fig. 7) differs in no essential from those of *Shorea* and *Chloroxylon*. The periods are continuous in a longitudinal direction; they are not accurately simultaneous; and the rate of change in inclination of the grain is not the same at different transverse levels in the same radial plane at the same moment resulting in the prominence of a period varying through the series.

In estimating the average period lengths and amplitudes in the longitudinal series, it was only possible to arrive at approximate values. The figures that were obtained showed that the period length and amplitude had their maximum value near the exterior but no gradual increase in value with age was shown as in *Shorea robusta*.

The disturbance caused by a small branch trace is shown very clearly in sticks 15, 16 and 17 of the longitudinal series. The branch trace passed horizontally outwards at the side of stick 16. The curves of sticks 15 and 17 show that as in straight-grained wood the grain as a whole curves round the knot retaining, however, its cross-grained character.

XYLIA DOLABRIFORMIS.

As the disc had already been used for a general investigation of the course of the grain, it was only possible to examine the course of the grain in detail in the plane of a radial board.

The data for the sticks of the longitudinal series are not printed here but the curves constructed from them are given in Fig. 8.

Taking the results obtained from the investigation of the disc in conjunction with the longitudinal series, it is clear that, as in the other species examined, the inclination of the grain as a whole alternates with growth between right-handed and left-handed, and also, as in the other species, the absence of complete contemporaneity of the periods at the various transverse levels and differences in the rate of change in the inclination of the grain at any moment, result in the grain consisting of a series of superposed serpentine curves.

HARDWICKIA BINATA.

In the transverse series the rings were counted accurately only as far as the 27th ring, after which only the more prominent rings lettered *V*, *W*, *X* and *Y* were traced round. In each stick the space between each two of these prominent rings was divided up into eight pseudo-growth rings of equal width. This procedure was adopted as the disc had not been smoothed sufficiently for tracing the fainter rings.

In the longitudinal series on the other hand the rings could be counted with precision from the centre to the exterior. As the board did not contain the pith the numbering of the rings in the two series does not correspond but as far as can be judged the 20th ring of the transverse and the 25th ring or the 26th ring of the longitudinal correspond.

An examination of the longitudinal and transverse series (Figs. 9 and 10) on the lines adopted for *Shorea robusta* and the other species shows that the serpentine grain of *Hardwickia binata* follows the same general rules as in the species already examined.

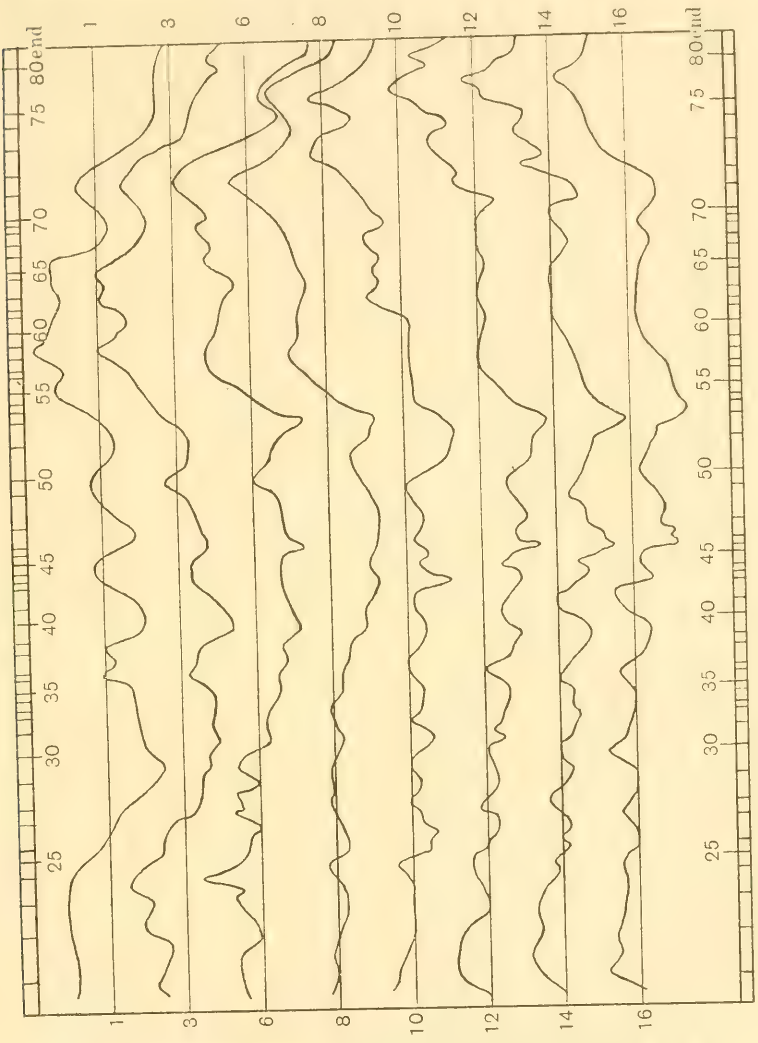


Fig. 9. *Hardwickia binata.* Longitudinal series. Same scale as Fig. 3.

In some respects the character of the grain differs from the typical form of serpentine cross-grain as shown in *Shorea robusta* and *Chloroxylon Swietenia*. The longitudinal and parallel zones are not readily distinguishable on a radial board which is due partly to the shortness of the period length and the comparatively small amplitude and partly to periods combining to form compound periods of big extent; stick 3 of the longitudinal series supplying a good example.

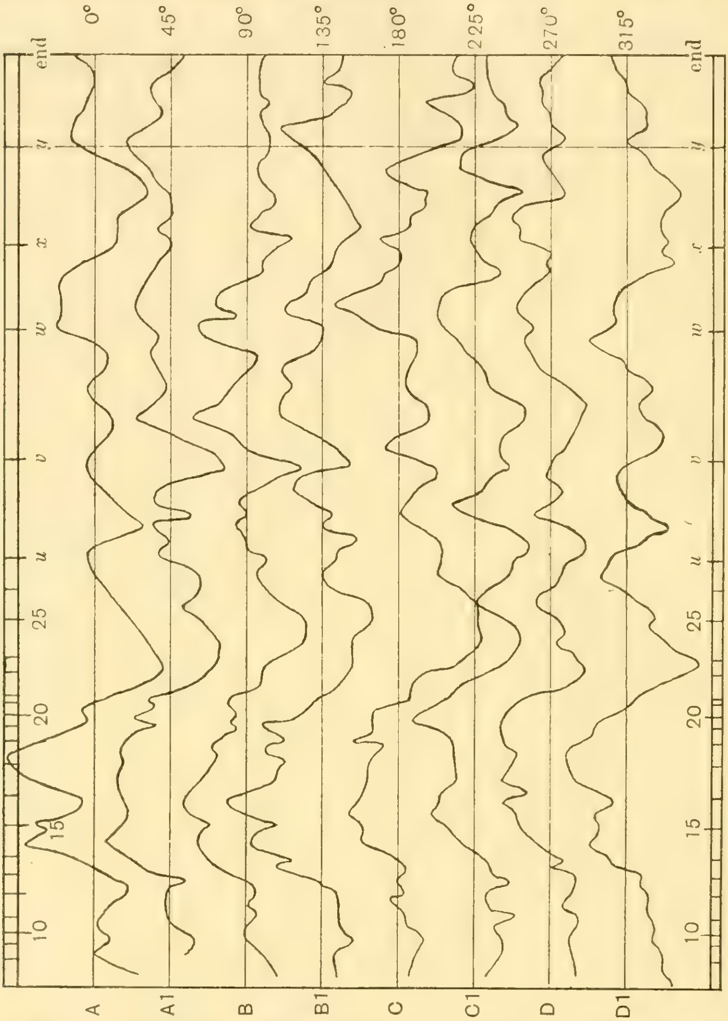


Fig. 10. *Hardwickia binata*. Transverse series. Same scale as Fig. 3.

Although, as the transverse series shows, these compound periods persist completely round at a transverse level, it seems that they are of only limited longitudinal extent.

CALOPHYLLUM[1] sp. POON.

For the material of this species I am indebted to Professor Groom for permission to saw a transverse section off each end of a six-foot beam of Poon wood, 10 inches by 3 inches in section, the longest side of the section being in a radial plane.

The rings were counted on both sections and to ensure identity in numbering every fifth ring was traced from end to end on the radial surface of the beam. The ring nearest the centre was numbered 1 but it was impossible to say how far it might have been from the centre, but the shape of the rings indicated that the beam had been sawn from near the outside of a very large trunk.

The numbering of the rings on the two sections only approximately correspond as difficulty was encountered in tracing the rings along the beam due to the rings frequently fading away, although in many cases they reappeared after a longer or shorter distance.

In Table VII are given the data derived from a radial stick sawn from each transverse section and the corresponding curves are shown in Fig. 11. The rings were plotted natural width and not to a scale of 2 to 1 as for the other species.

The striking feature of Poon wood is the great length of the period (8½ cms.), being a little more than twice that of *Shorea robusta.* In another specimen of Poon, and probably of the same species, having the same number, four, of rings per centimetre, the period length was 6 cms. This fact suggests that a study of double cross-grain with reference to soil and climate would yield interesting results.

If the rings are used as an index of contemporaneity, though this is somewhat open to doubt for Poon wood, it is seen that the periodic changes in the inclination of the grain are practically simultaneous through a length of six feet, contrasting with the comparatively big shift in the position of some of the periods of the longitudinal series of *Shorea robusta* and *Xylia dolabriformis.*

Judging from the contemporaneity of the periods and the slight variation in their amplitude at the two levels it is to be inferred that the grain in Poon is a true double spiral.

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[1] The specific identity of the wood examined was doubtful, though it bore the name of Poon, which belongs to *Calophyllum tomentosum.*

Table VII. *Calophyllum* sp. Spacing of rings in cms. and inclination of grain in degrees along two radial sticks in same radial plane and six feet apart.

No. of ring	Bottom stick		Top stick	
	cms.		cms.	
$n+0$	0	4½/	0	—
$n+1$	·01	7 /	·20	*v*
$n+2$	·35	5 /	·30	4½\
3	·50	3½/	·60	6½\
4	·70	1 /	·85	*v*
5	1·10	2 \	1·10	½\
6	1·40	3½\	1·40	2 \
7	1·60	5 \	1·65	4 \
8	1·80	5 \	1·75	3 \
9	2·10	6 \	1·90	6 \
10	2·35	8½\	2·20	8 \
11	2·70	10 \	2·45	9 \
12	3·00	7 \	2·70	7½\
13	3·40	9 \	2·95	6 \
14	3·70	9 \	3·20	6 \
15	4·20	7 \	3·45	5 \
16	4·70	4 \	3·90	*v*
17	5·10	2 \	4·15	6½/
18	5·30	*v*	4·30	7½/
19	5·60	1½/	4·50	7½/
20	5·90	1 /	4·65	9½/
21	6·30	2½/	5·00	11½/
22	6·60	6 /	5·40	13½/
23	6·90	11 /	5·80	11 /
24	7·25	11½/	6·30	8½/
25	7·65	10 /	6·70	5 /
26	8·00	9 /	7·20	3 /
27	8·30	7 /	7·50	*v*
28	8·60	5 /	7·85	2 \
29	8·90	1½/	8·15	3 \
30	9·15	*v*	8·45	4 \
31	9·45	2 \	8·75	5 \
32	9·65	3 \	9·00	7 \
33	9·85	2 \	9·30	9 \
34	10·10	2½\	9·60	7½\
35	10·35	6½\	9·80	13 \
36	10·70	6 \	10·00	11 \
37	10·90	5 \	10·30	11 \
38	11·10	8½\	10·60	9½\
39	11·30	10 \	10·90	8 \
40	11·55	10 \	11·20	6½\
41	11·70	9 \	11·60	—
42	11·85	8½\	11·80	3 \
43	12·20	8½\	12·20	2 \
44	12·60	6 \	12·50	2 /
45	12·90	6 \	12·80	4 /
$n+46$	13·15	3 \	13·00	5 /
47	13·40	2½\	13·30	6 /
48	13·80	2½/	13·55	8 /
49	14·00	5 /	13·85	8½/
50	14·20	7½/	14·00	11½/
51	14·50	7½/	14·20	13 /
52	14·75	6½/	14·40	12½/
53	15·00	6½/	14·60	10 /
54	15·25	9 /	14·70	8½/
55	15·50	10 /	14·90	8 /
56	15·65	6½/	15·05	4½/
57	15·90	2 /	15·25	4 /
58	16·10	1 \	15·50	3 /
59	16·25	1½\	15·70	2 /
60	16·50	2½\	15·90	3 \
61	16·85	4 \	16·00	2½\
62	17·00	4½\	16·20	4½\
63	17·10	7 \	16·40	6½\
64	17·25	5½\	16·70	6 \
65	17·45	5½\	16·90	4½\
66	17·70	7½\	17·05	7½\
67	17·90	8½\	17·25	9 \
68	18·15	10½\	17·45	11 \
69	18·40	11 \	17·85	14½\
70	18·50	9½\	18·10	11 \
71	18·75	11½\	18·30	11 \
72	19·00	13½\	18·55	9½\
73	19·25	14 \	18·70	7 \
74	19·50	15½\	18·85	5 \
75	19·80	15 \	19·05	3½\
76	20·00	11 \	19·25	1½\
77	20·20	7 \	19·55	3 /
78	20·40	7 \	19·80	3½/
79	20·65	4 \	19·95	3 /
80	20·85	3 \	20·10	4 /
81			20·25	3 /
82			20·40	4½/
83			20·70	5 /
84			20·90	8½/
85			21·10	7 /
86			21·30	9 /
87			21·45	12½/
88			21·65	14 /
89			21·85	9 /
$n+90$			22·05	9½/

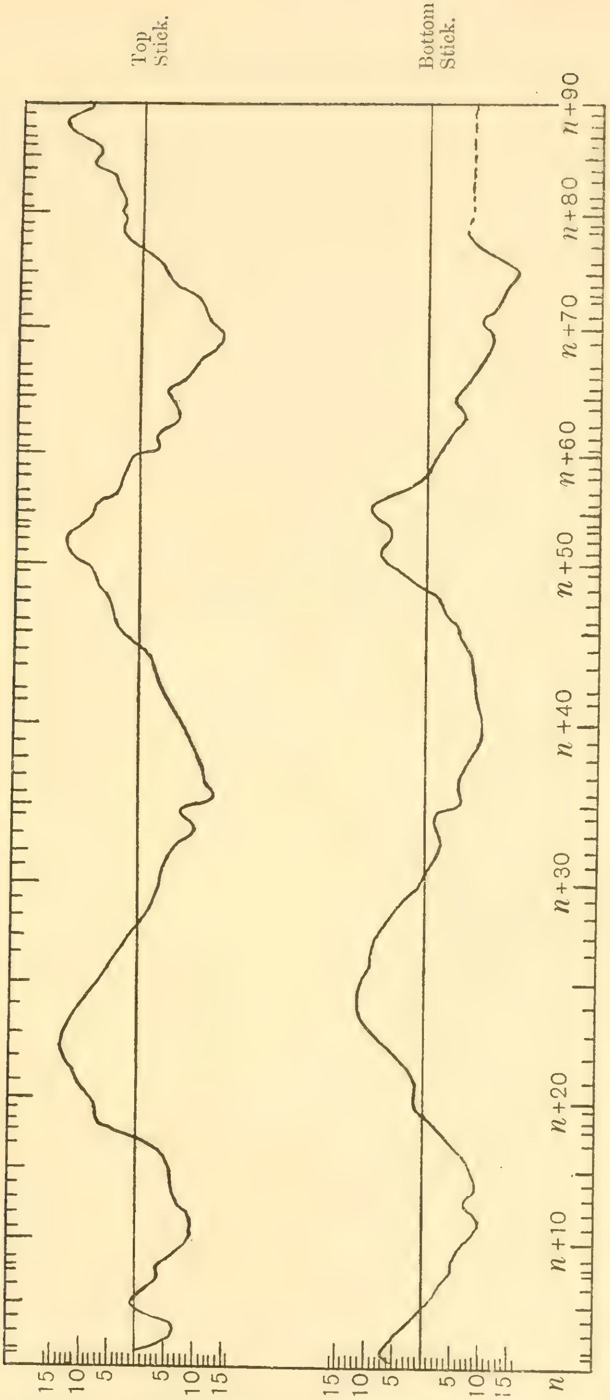

Fig. 11. *Calophyllum* sp. Two curves showing inclination of the grain in two radial sticks six feet apart and in the same radial plane. Rings numbered from "n" to "$n+90$." Scale: rings plotted natural width and angles of inclination 1 mm. to 1 degree.

Remaining Species.

All the remaining species were examined by the method of radial fracture alone. In no case was any type of cross-grain discovered which did not agree in essentials with that which is characteristic of the species examined in detail.

Even in the straight-grained *Albizzia procera*, slight variations in the grain, too small to be investigated by the detailed method, could be detected which conformed to the same general laws which applied to *Shorea robusta*, etc.

In Fig. IV, of the Plate, are shown the fractures obtained in a portion of the transverse disc of *Holoptelea integrifolia* and, in Fig. V, the fractures in the longitudinal series of sticks.

GENERAL CONSIDERATIONS.

During the course of this investigation several points stood out with sufficient prominence to merit a short discussion anent their probable significance.

The wide distribution of double cross-grain and the uniformity of its character among trees of the most diverse natural orders suggest that it is the expression of some peculiarity common to a large circle of affinity in the vegetable kingdom.

The long series of intermediate forms between straight grain and the full expression of double cross-grain reached by the serpentine cross-grain of *Shorea robusta* and the probable double spiral of *Calophyllum*, and the variation in its development among the members of the same family (see Fig. 1), suggest that there is something, whether of internal or external nature, that inhibits or enhances the expression of double cross-grain, but for the formation of a correct judgment on this point, research is necessary on the influence of local conditions of soil and climate on the development of this type of grain.

There may be, possibly, some correlation between a hot climate and the prevalence of this type of grain, but this can only remain a supposition until temperate climate trees and a larger number of trees from hot climates have been examined from this point of view.

In the attempt to place double cross-grain in proper perspective with reference to other phenomena shown by living objects, a close similarity was found to exist between the changes in the inclination of the grain and the phenomenon of periodicity.

Periodic phenomena among living organisms can be classed under two heads. Under "Induced Periodicity" are included all those cases which show a more or less direct correlation with the rhythm in external conditions: for instance diurnal and seasonal changes are reflected in the periodicity shown by growth and leaf-fall.

Under "Innate Periodicity" are included all those cases in which no correlation can be demonstrated to exist between the rhythm shown by a living object and the rhythm in external conditions, examples being the alternating streaming movements of the protoplasm of Myxomycetes and the leaf-fall of trees of tropical climates which are characterised by, at the most, only feebly marked seasonal changes (Schimper(4)).

It is under this latter head that the phenomenon of double cross-grain naturally falls for, relying on the evidence of the rings, no correlation could be established between seasonal changes and the period of the grain.

Some interesting analogies are shown between double cross-grain and the leaf-fall of trees native of regions showing absence of seasonal changes (see Schimper). Corresponding with the full development of double cross-grain are those trees which completely shed their foliage at regular intervals varying from two to twelve months, irrespective of the time of year. Trees in which the periodicity of the cross-grain is synchronous only within narrow limits in the trunk are paralleled by those trees which, considered as a whole, are evergreen, but in which the individual twigs are alternately bare and clothed with foliage.

If this type of grain is the expression of some periodicity in the life processes, it is to be expected that other periodic variations, synchronous with the variations in the inclination of the grain should be found. With this object in view the fibre lengths in *Chloroxylon Swietenia* and in *Calophyllum* were determined along a stick at points where the grain was straight and where it was inclined at a maximum.

The figures which are shown in Table VIII are very suggestive, but the inference that there is a correlation between a longer fibre length and inclined grain has no very sound statistical basis for 500 is not a large enough basis for determining a mean where the deviation from the mean is so large in comparison to the difference in the mean fibre length of the successive samples.

Since very little is known of the mechanical effects due to the increase in length of the young fibres it is impossible to say whether the changes in the inclination of the grain might be directly attributable to a variation in fibre length such as is indicated above. The impression obtained, however, during the course of the investigation was that the changes in the inclination of the grain were due to changes in the orientation of the cambial cells and that the fibres elongated in the direction in which they were laid down when cut off from the cambial cells and that it was not exigencies of spaces that caused their deviation from the straight.

Table VIII. *Chloroxylon Swietenia.* Variation in the mean fibre length with inclination of the grain.

Ring and direction of inclination of grain	76th/	78th *v*	83rd\	85th *v*	88th/	92nd *v*	94th\	97th *v*	99th/
Basis (number of fibres measured)	502	400	500	496	500	600	288	507	530
Mean fibre length in mms. ...	1·050	1·02	·965	·982	·990	·954	1·040	·968	1·030
Mean deviation from mean fibre length in mms. ...	·125	·151	·123	·145	·140	·159	·160	·137	·110
% of fibres within the mean deviation	54	54	53	60	57	58	53	58	57
	108th *v*	112th/	118th *v*	124th\	132nd *v*	140th\	144th *v*	148th/	150th *v*
Basis (number of fibres measured)	500	515	424	330	314	468	459	382	481
Mean fibre length in mms. ...	·935	·875	·845	·900	·817	·844	·826	·854	·847
Mean deviation from mean fibre length in mms. ...	·107	·102	·109	·110	·100	·105	·82	·102	·110
% of fibres within the mean deviation	59	56	56	57	57	57	57	57	56

Table IX. *Calophyllum* sp. Variation in the mean fibre length.

Ring and direction of inclination of grain	$(n+3)$th \	$(n+10)$th *v*	$(n+17)$th /	$(n+25)$th *v*	$(n+34)$th \	$(n+37)$th *v*
Basis (number of fibres measured)	100	100	100	100	100	100
Mean fibre length in mms.	1·160	1·080	1·160	1·020	1·140	1·110
Max. fibre length in mms.	1·710	1·460	1·660	1·450	1·610	1·800
Min. fibre length in mms.	·780	·760	·810	·680	·840	·790

With regard to its commercial aspect the economic value of a study of cross-grain lies in its application in the practice of seasoning wood. The main problems in the seasoning of wood centre round the differences in the rate of loss of moisture and in shrinkage during drying in radial, tangential and longitudinal directions, hence knowledge of the degree of cross-grain shown by different woods is essential if the economic mean between care expended and time involved is to be gauged.

SUMMARY.

1. The character of the double cross-grain of the different Indian woods examined is remarkably uniform and conforms to the following generalisations:

(*a*) The grain alternates between right-handed and left-handed in inclination during the growth of the tree, these changes in the inclination being in general synchronous in the trunk at least over lengths of two feet.

(*b*) That the grain does not consist of alternate right- and left-handed spirals is due to the rate of change in inclination of the grain not being uniform at any moment during the growth of the tree either in a tangential or longitudinal direction with the result that the double spiral character is obscured, giving place to a serpentine configuration.

2. Transitional types of grain between straight grain and the full development of double cross-grain are due to variations in the—

(*a*) regularity shown in the length of the successive periods,
(*b*) regularity in the amplitude of the successive periods,
(*c*) stability of the periods over longer or shorter tangential and longitudinal distances.

3. No correlation could be inferred, from the data available, as existing between seasonal changes or periods of growth and the periodicity shown in the inclination of the grain.

There were indications, however, that both period length and amplitude increased with age up to a maximum, and that a long period length was correlated with a big amplitude. Period length responds to the general rate of growth for, in trees of excentric growth, the period length was shortest along the smallest radius.

4. Fibre measurements in *Calophyllum* sp. and *Chloroxylon Swietenia* suggest that a longer fibre length is correlated with inclined grain and a shorter fibre length with straight grain.

5. The character and widespread occurrence of double cross-grain indicate that it is the expression of some periodic phenomenon whether of internal or external nature, but it remains to be seen to what extent a more extended investigation will bring it into line with other periodic phenomena shown by living organisms.

This research was carried out in the Woods and Fibres Department of the Imperial College of Science and Technology, South Kensington, while the author was in receipt of a studentship from the Department of Scientific and Industrial Research.

In conclusion I wish to record my thanks to Professor Percy Groom for suggesting this investigation, providing the material and for help throughout the progress of the work.

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(4) SCHIMPER, A. F. W. *Plant-Geography.* English edition, 1903.

DESCRIPTION OF PLATE XIII

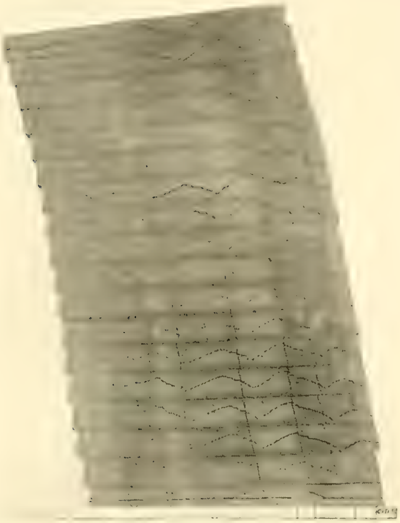
I. *Shorea robusta.* The series of fractures obtained by radially splitting sticks sawn transversely an inch broad, from an 18 inch radial board. Several of the more prominent rings inked over.

II. *Chloroxylon Swietenia.* Prepared as in I.

III. *Gmelina arborea.* Radial fractures obtained in a portion of the transverse disc. Several rings inked in.

IV. *Holoptelea integrifolia.* Radial fractures in a portion of the transverse disc.

V. *Holoptelea integrifolia.* Longitudinal series of fractures prepared as in I.



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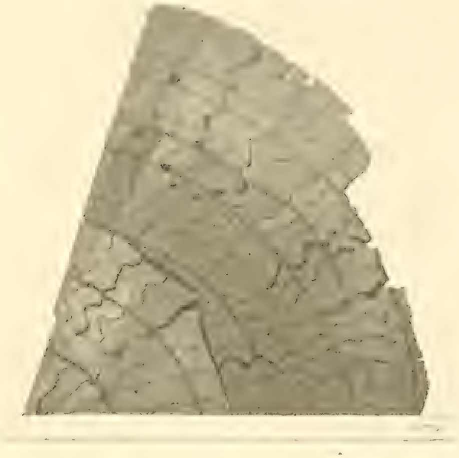

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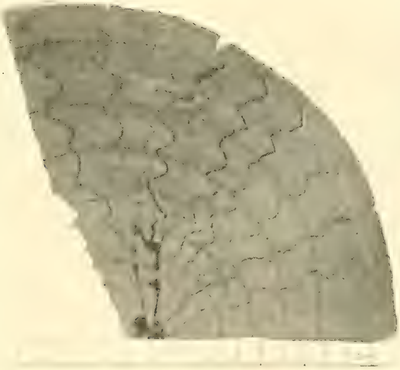

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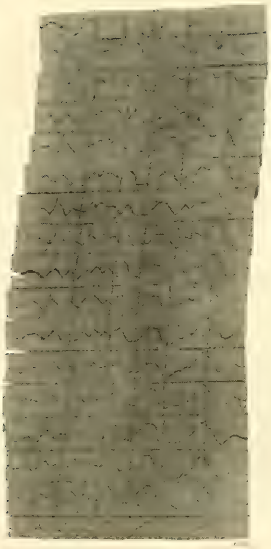

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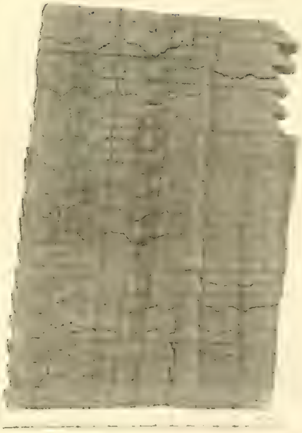

V

BIONOMICS OF WEEVILS OF THE GENUS SITONES INJURIOUS TO LEGUMINOUS CROPS IN BRITAIN.

By DOROTHY J. JACKSON, F.E.S.

(With Plates XIV–XIX and 6 Text-figures.)

Read by Dr R. Stewart MacDougall, *July 3rd*, 1919.

PART I.

INTRODUCTORY.

It is well known that weevils of the genus Sitones are serious pests of leguminous crops throughout the world. Their depredations have been recorded on every species of clover, on vetches, lucerne, peas, beans and lupins. The adults injure the plants by eating the leaves, and crops of peas and beans in their early stages are often destroyed in this manner.

Further damage is also done to the plant by the larvae which feed upon the roots. In the case of peas and beans the larvae are especially destructive to the root nodules which are of such value to the plant on account of the nitrogen fixing bacteria which they contain.

In Great Britain there are several injurious species of Sitones. The damage done by *S. lineatus* has been fully related by Miss Ormerod in her *Reports on Injurious Insects* (11) but of the regular though less striking toll effected by many of the other species on clover fields throughout Great Britain much less is known.

Examination of the existing literature on Sitones revealed the fact that despite the wide distribution and the destructive habits of these insects, the life-history of no single species in Great Britain was completely known, not even that of *Sitones lineatus*. Many records and observations on Sitones were collected by Miss Ormerod, but unfortunately in the majority of cases no attempt was made to establish the identity of the species to which the information referred, with the result that one can gain from her *Reports* very little definite information on any one particular species. As a thorough knowledge of the life-history of a pest is essential to its successful control the genus Sitones appeared to me to offer a field for investigation. I have therefore attempted to find out the life-history of the different species which abound on leguminous crops in Britain, and at the same time to ascertain the nature and extent of the damage done by each in both the larval and adult stages. I have only concerned myself with those species which I have found present on crops in sufficient number to cause injury and these consist of the following: *S. lineatus* L., *puncticollis* Steph., *flavescens* Marsh., *sulcifrons* Thun., *hispidulus* F., *humeralis* Steph. and *crinitus* Herbst.

By means of the following key which I have adapted with some alterations from Fowler's (15) I have endeavoured to make it easier to distinguish each injurious species from the other and also from the remaining species of the genus. As it is exceedingly difficult to form a satisfactory table to separate species which have such a close general resemblance I add figures of the species concerned which I hope will supplement the key. Each species will be described in detail when dealt with.

Key to the British Species of the Genus Sitones found on Leguminous Crops[1].

(The injurious species are marked with an asterisk.)

I. Size large 6–9 mm.; elytra long and tapering towards the extremity which is pointed. Scutellum usually very conspicuous with two white tufts of hair which diverge in front and cause it to appear emarginate . . . . *S. griseus* F.

II. Size 2–6 mm.; if large, elytra not relatively long or tapering towards extremity.

- i. Elytra, if viewed sideways, with very distinct raised setae which are more or less erect.
  - 1. Thorax convex and arched forming a distinct angle with the elytra if viewed sideways, sides of thorax strongly rounded; eyes prominent; outstanding setae very long . . . . *S. regensteinensis* Herbst.
  - 2. Thorax not convex or arched, almost on same level as elytra.
    - A. Eyes flat, body thickset and compact, thorax with large diffuse punctures and the sides moderately strongly rounded **S. hispidulus* F. (Plate XIV, Fig. 6).
    - B. Eyes very prominent. Thorax with sides slightly rounded.
      - *a.* Eyes extremely prominent projecting almost on a line with the shoulders, bristles a little more depressed, scales of elytra narrower, punctuation of thorax coarser and more diffuse . . . . *S. Waterhousei* Walt.
      - *b.* Eyes prominent but not projecting nearly to line of shoulders; scales of elytra broader and bristles more erect; punctuation of thorax finer and closer . . . . **S. crinitus* Herbst. (Fig. 3).
- ii. Elytra, if viewed sideways, with fine raised setae or hairs which are depressed towards the apex but are distinct from the general pubescence. Size small,

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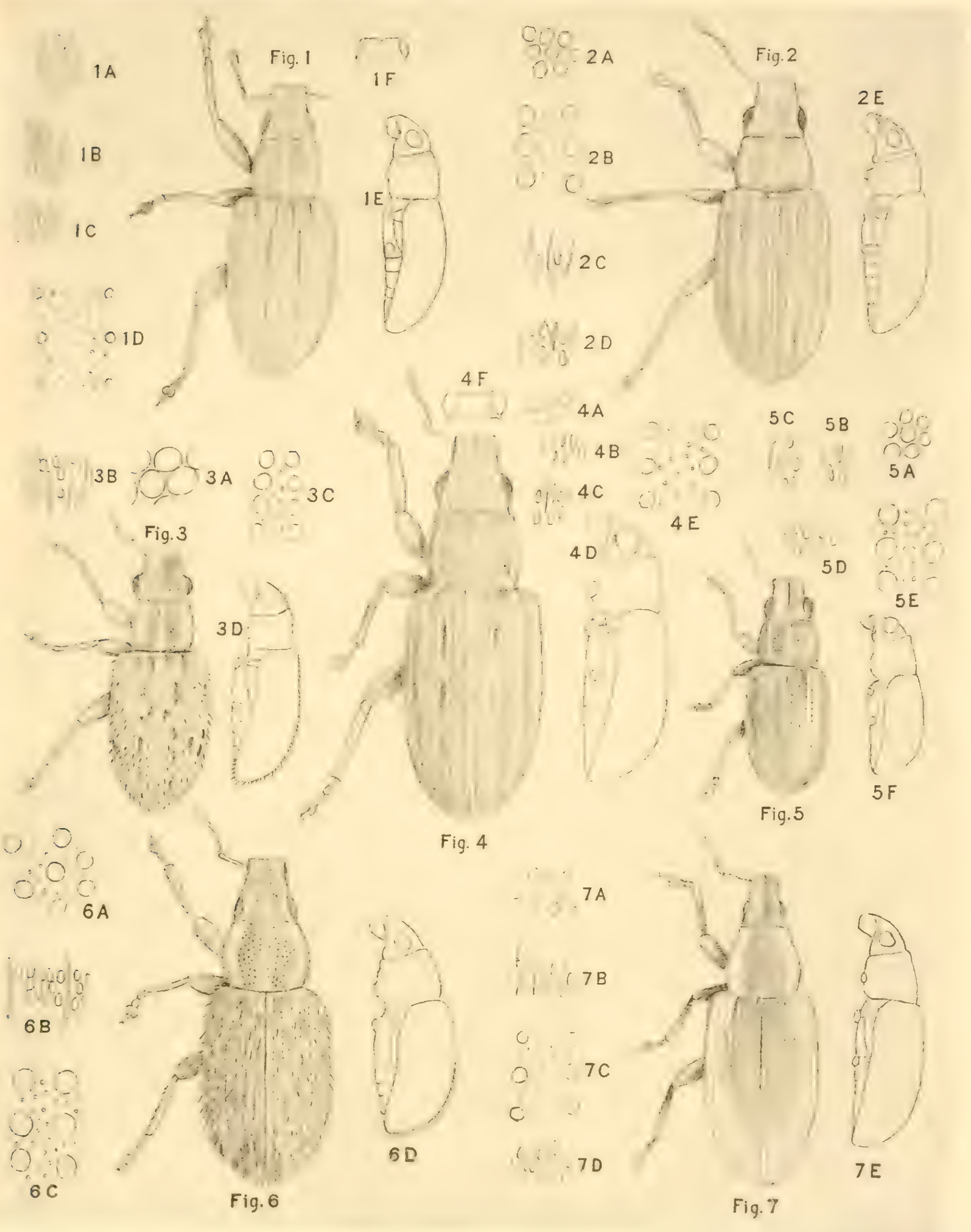
[1] *S. cylindricollis* Fåhraeus (= *meliloti* Walton) has been omitted from this key on account of its scanty distribution and local habits.



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Weevils of the genus Sitones injurious to Leguminous crops in Britain $\times 8\frac{3}{4}$.

Fig. 1. *S. flavescens* Marsh. 1 A = punctuation of thorax, 1 B = scales of thorax, 1 C = scales of elytra, 1 D = punctuation of elytra, 1 E = side view of weevil, 1 F = forehead viewed from above.

Fig. 2. *S. lineatus* L. 2 A = punctuation of thorax, 2 B = punctuation of elytra, 2 C = scales and setae of thorax, 2 D = scales and setae of elytra, 2 E = side view of weevil.

Fig. 3. *S. crinitus* Herbst. 3 A = punctuation of thorax, 3 B = scales and setae of elytra, 3 C = punctuation of elytra, 3 D = side view of weevil.

Fig. 4. *S. puncticollis* Steph. 4 A = punctuation of thorax, 4 B = scales and setae of thorax, 4 C = scales and setae of elytra, 4 D = side view of weevil, 4 E = punctuation of elytra, 4 F = forehead viewed from above.

Fig. 5. *S. sulcifrons* Thunb. 5 A = punctuation of thorax, 5 B = scales and setae of thorax, 5 C = scales and setae of elytra, 5 D = scales from sides of body, 5 E = punctuation of elytra, 5 F = side view of weevil.

Fig. 6. *S. hispidulus* F. 6 A = punctuation of thorax, 6 B = scales and setae of elytra, 6 C = punctuation of elytra, 6 D = side view of weevil.

Fig. 7. *S. humeralis* Steph. 7 A = punctuation of thorax, 7 B = scales and setae of thorax, 7 C = punctuation of elytra, 7 D = scales and setae of elytra, 7 E = side view of weevil.

3–4 mm., elytra rather short and broad, widest across the middle and narrowed anteriorly *S. lineellus* Gyll, and *S. tibialis* Herbst. (= *brevicollis* Brit. Cat.).

iii. Elytra without upstanding setae.

1. Dorsal portion of elytra without scales but entirely clothed with fine flat hairs or setae. Size comparatively large, 5–6 mm.; thorax with very large punctures and the sides strongly rounded and dilated *S. cambricus* Steph.

2. Dorsal portion of elytra more or less completely covered with scales interspersed with flat hairs of setae which are rarely absent.

A. Elytra with the sides almost straight, parallel and not becoming wider behind the shoulders, and with the dorsal area when viewed sideways only slightly curved.

a. Width of head across eyes almost equal to width of pronotum.

aa. Elytra moderately long, with distinct, moderately long, almost flat setae evenly distributed amongst the scales and not arranged in groups, pronotum comparatively short, rostrum with central dorsal groove continued between the eyes, size 4–5 mm.
*S. *lineatus* L. (Fig. 2).

bb. Elytra shorter, setae shorter and principally arranged irregularly in groups, pronotum comparatively longer, central groove of rostrum not continued between the eyes. Size 6 mm.
*S. *puncticollis* Steph. (Fig. 4).

b. Width of head across eyes distinctly narrower than width of pronotum. Head deeply excavated between the eyes. Shoulders usually with a conspicuous patch of pale scales . . . *S. *humeralis* Steph. (Fig. 7).

B. Elytra with the sides more or less rounded and the greatest width near the middle, and with the dorsal area distinctly curved when viewed sideways.

a. Head not excavated between the eyes but with a central groove, size 4 to 5½ mm.

aa. Scales ochreous or ochreous brown, thorax very finely and shallowly punctured . . . . *S. *flavescens* Marsh. (Fig. 1).

bb. Scales coppery red or metallic greenish, punctures on thorax fine but coarser than *flavescens*
S. suturalis Steph. (and var. *ononides* Sharp).

b. Head deeply excavated between the eyes; size small, 2½–3 mm., elytra sparingly covered with scales; a conspicuous patch of white scales on the sides of the thorax and anterior abdominal segments
*S. *sulcifrons* Thün. (Fig. 5)

I propose to deal in detail with the species *seriatim* taking first *S. lineatus* to which the remainder of this paper is devoted.

SITONES LINEATUS L.

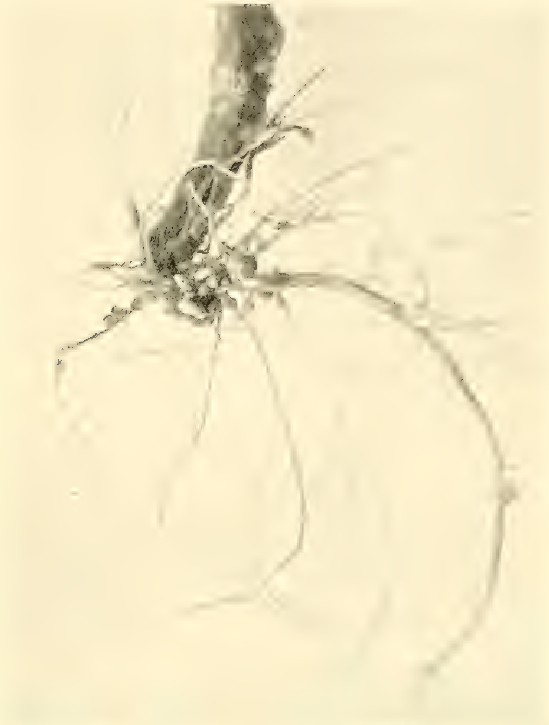
In 1761 this species was described by Linnaeus (1) who records it as being common in gardens and fields. It is now a well-known pest of leguminous crops and is widely distributed throughout Europe. It is common throughout the British Isles but is less destructive in the north of Scotland than in the south of England.

FOOD-PLANTS.

Peas, beans, lucerne (*Medicago sativa*), medick (*Medicago lupulina*), all species of clover (*Trifolium*), tares (*Vicia sativa*), and wild vetches.

In Britain this is the most abundant species infesting peas and beans and is only too well known in consequence. I have noticed that it greatly prefers peas, beans and vetches to clover, thus wild vetches growing in fields of clover are often almost denuded of leaves by this species while the clover growing round it is not touched. Similarly comparatively few specimens are to be taken in clover fields if peas and beans are growing in the vicinity, though from October until April this species is common upon clover. On the other hand I have found this species abundant on lucerne throughout the year. It would thus appear that clover is not the favourite food-plant of this species but only resorted to when the others are unobtainable. This view is further supported by examination of the life-history which seems to be specially adapted to peas and beans, as egg laying only takes place during spring or summer when the peas and beans are in a condition to support the resultant larvae.

Other recorded food-plants. E. M. Vassiliev in *Ent. Section of the Rep. of the Exp. Ent. St. of all Russ. Soc. of Sugar Refiners for* 1914, Kiev, 1913, pp. 12–23, Abstract *Rev. App. Ent.* A. I (1913), pp. 485 and 487, mentions the occurrence of *S. lineatus* on vines and sugar-beet, though he records it as not a pest of the latter; A. Tullgren in "Skadedjur i Sverige Åren 1912–1916" (Injurious Animals in Sweden during 1912–1916), *Meddelande från Centralanstalten för Jorsbruksförsok*, No. 152, *Entomologiska avdelningen*, No. 27, p. 104, Abstract *Rev. App. Ent.* VI (1918), p. 147, observes that *S. lineatus* damages raspberries; E. Molz and D. Schroder (18) record an attack of *S. lineatus* on chicory and mentions beet being damaged by the larvae. Bargagli (16) records as food-plants of this species *Ilex aquifolium* and *Pinus sylvestris*; the latter tree is also recorded by Taschenburg (12) as a habitat of *S. lineatus* but I have no doubt that the weevils were merely sheltering in these trees. I have met with no corroborative evidence of *S. lineatus* occurring on vines, raspberries, chicory or sugar-beet in this country.



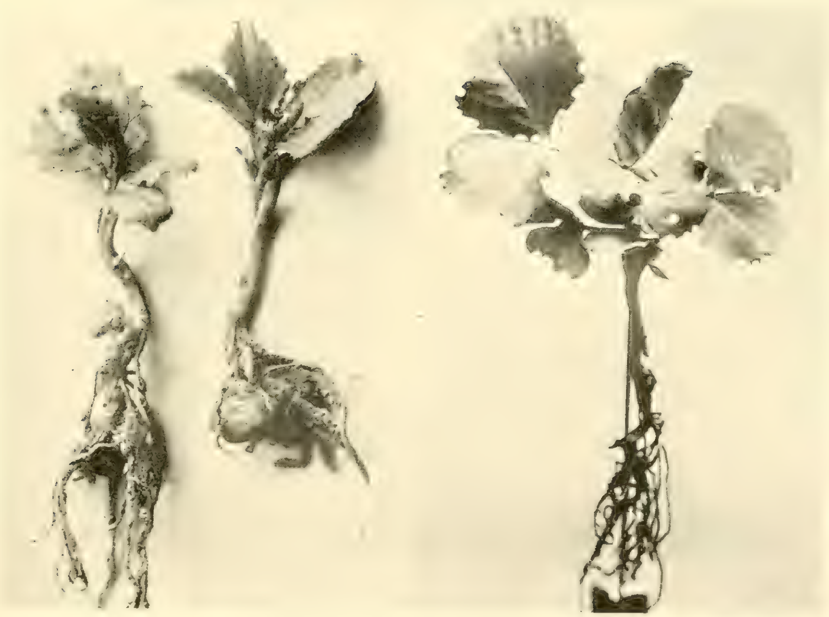


Fig. 1. Root of bean plant, showing larvae of *Sitones lineatus* feeding on root nodules.
Fig. 2. Bean plants with leaves damaged by adult of *S. lineatus*.
Fig. 3. Pea plant ditto.

NATURE OF DAMAGE.

I. *Damage by Adult.* (Plate XV, figs. 2 and 3.)

The adult weevils do principal damage to peas and beans when the plants are from 3 to 6 inches high. They feed upon the leaves in a characteristic way. Commencing always at the edge of the leaf they eat U-shaped notches out of it. In the young leaves which are still folded they do the same, thereby forming a notch on each side of the leaf. These notched leaves are typical of the first appearance of the weevil and this stage of the attack is illustrated in the accompanying figures. If many weevils are present and especially if the growth of the plant is at all checked through cold or drought the young leaves and growing shoots are more or less completely eaten away thereby causing great reduction or complete loss of the crop. Miss Ormerod states many instances of farmers having to plough up their pea crops on this account, and the Board of Agriculture (22) records the complete destruction of pea and bean crops in many places during 1917, through the severe attack of this pest.

II. *Damage by Larvae.* (Plate XV, fig. 1.)

The damage effected by the larvae consists chiefly in attacks on the root nodules of peas and beans. This destruction attains its maximum at the commencement of the flowering season. The nodules in all stages of growth are excavated by the larvae and although new nodular growths often develop these also are destroyed by the larvae. After a severe attack only the hollowed out shrunken skins remain; and the nodules are thus often completely destroyed at a critical stage of the plants' development.

Description of Adult. (Plate XIV, fig. 2.)

Black, clothed on the dorsal surface with brownish ochreous or greyish ochreous scales interspersed with flat setae, frequently arranged on the elytra in the form of darker and lighter longitudinal stripes. Under-surface covered with whitish grey scales. Size 3·6 to 5·4 mm.

Build. Head moderately broad between the eyes which are slightly prominent, projecting beyond the line of the sides of the anterior part of the pronotum. Rostrum with a central furrow which is continued between the eyes, but the area between the eyes traversed by the furrow is otherwise level. Pronotum broader than long, the sides rounded, the anterior edge very slightly raised so as to form a narrow rim or collar. Elytra long and with parallel sides, not increasing in width behind the shoulders but continuing of equal width for two-thirds of their length, then gradually tapering towards the extremity which is oval. The shoulders are moderately prominent. When viewed from the side the elytra are seen to be almost level along the back.

Pubescence and sculpturing. The *pronotum* is covered with medium sized punctures rather closely placed. It bears numbers of pale coloured setae, the points of which are directed anteriorly and only very slightly raised. These setae increase in size towards the anterior margin of the pronotum. Sparingly distributed amongst the setae are scales which vary in colour in the different specimens, being reddish ochreous, brownish ochreous or greyish ochreous. These scales are larger and more closely placed in a line along the middle and on a broader band on either side, thus giving rise to light dorsal and sub-dorsal stripes. The scales are moderately large, spatulate and forwardly directed.

The *elytra* have distinct punctured striae, the interstices being marked by very minute sculptured dots. The elytra are closely covered with scales similar to the pronotum but backwardly directed. The scales are of varying colours and are frequently arranged in alternate stripes of light and dark, silvery grey or silvery ochreous. Evenly interspersed with the scales are light coloured setae, flat, and backwardly directed; but becoming longer and slightly more raised towards the extremity of the elytra. These setae are paler and more conspicuous on the alternate striae corresponding with the colour of the scales forming the light coloured stripes.

The sides and under-surface of the body are clothed with whitish grey scales which are frequently tinted with pink. They are larger than those on the dorsal surface and of various shapes and are interspersed with flat setae on the sternites of the thorax and abdomen.

The legs. The femora are black but reddish at the base and extreme apex, clothed with pale ochreous scales and long pale setae, the tibiae and tarsi are light brownish red clothed with long white setae.

The *antennae* are rather long and slender, brownish red with fine pale hairs.

External Sexual Differences between Male and Female.

The sexes can be distinguished by examination of the posterior abdominal segments. The differences are most apparent when the elytra and wings have been removed, but it is possible to differentiate live specimens by examination of the ventral surface only. On the dorsal surface of the abdomen in both sexes eight tergites are present. The seventh abdominal tergite is known as the propygidium, the eighth as the pygidium. In both sexes the propygidium bears short bristles posteriorly whilst the pygidium is covered with them. The preceding tergites are devoid of bristles. On the ventral surface of the abdomen in both sexes are five visible sternites. According to Hopkins' account[1] of the sternites of beetles of the genus Dendroctonus these five sternites may be taken to represent sternites 3 to 7, as the first and second are stated by him to be obscured by the coxal cavity and probably this explanation holds good for Sitones also. The area on the sides between the tergites and sternites is occupied by the pleurites. These consist of a more dorsal line of membranous pieces, the epipleurites, which contain the spiracles, and below them a line of chitinous pieces called the hypopleurites. The pleurites are normally covered by the elytra. The external sexual differences are to be found in the shape of the pygidium and the hypopleurites and sternite of the last segment.

The Male. (See Fig. II[2], IV and VI, p. 276.)

The pygidium is much larger than in the female and completely overlaps the ends of the hypopleurites of each side. The hypopleurite of the last segment is shorter than in the female and ends abruptly where it touches the pygidium and is not continued round the end of the body as a narrow edge dorsal to the sternite. The sternite of the last segment has the edge truncated and not rounded. This point must be examined carefully, for if hastily viewed with a lens the extremity of the sternite of the male often appears as round as that of the female owing to the rounded edge of the pygidium being closely applied to the sternite more or less obliterating the anal orifice which occurs between them.

The anal opening occurs between the pygidium and the seventh sternite.

The Female. (See Fig. I[2], III and V, p. 276.)

Pygidium much smaller than in the male and not overlapping the hypopleurite. Hypopleurite of the last segment longer than in the male, not ending abruptly but gradually narrowing to a small ridge which is continued round the end of the body above the seventh sternite to join with the hypopleurite of the other side. Seventh sternite with the extremity evenly rounded. Anal orifice occurring between the pygidium and the ridge of the hypopleurite.

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[1] "The Genus Dendroctonus," by A. D. Hopkins, *U.S. Dept. Agric. Bur. Ent. Technical Series*, No. 17, *Bulletin* No. 83, Part 1, June 1909.

[2] To simplify these illustrations I have omitted scales, bristles and sculpturing.

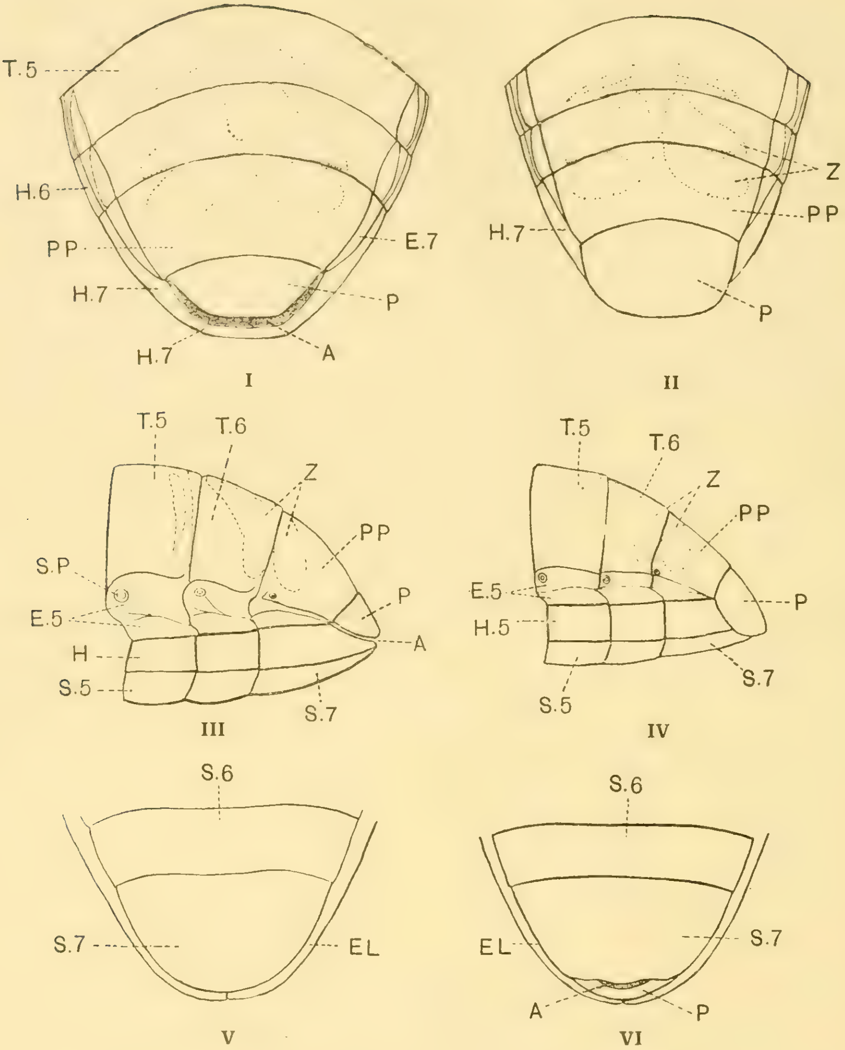
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Fig. 1. Posterior abdominal segments of weevils of *S. lineatus* ×31.

I. Female viewed dorsally with elytra removed.
II. Male viewed dorsally with elytra removed.
III. Female viewed laterally with elytra removed.
IV. Male viewed laterally with elytra removed.
V. Female viewed ventrally.
VI. Male viewed ventrally.

A = anus; E = epipleurite; EL = elytra; H = hypopleurite; P = pygidium; S = sternite; SP = spiracle; T = tergite; Z = pubescent area. The numbers following the letters refer to the segments, *e.g.* T. 6 = tergite of 6th segment.

Sexual differences in the legs. A very slight difference occurs between the legs of the male and female. In the male there is a small pointed prominence at the apex of the tibiae of all the legs on the inner side, but it is most conspicuous on the anterior tibiae. In the female though a slight prominence occurs on the same place it is much smaller on all the legs than in the male. As in both sexes the apex of the tibia is much obscured by long bristles this difference is difficult to ascertain in uncleared specimens and I merely mention it as the presence of a "hook" on the anterior tibiae of the male is given by Fowler (15) as a character for distinguishing the male of this species.

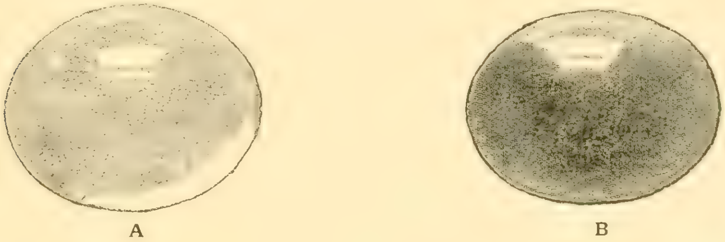

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Fig. 2. Eggs of *Sitones lineatus* L. × 91.
A = newly laid egg.
B = egg a few days later.

The Egg. (Fig. 2.)

The eggs viewed with a lens are smooth, but under a microscope their surface is seen to be slightly roughened. In shape they are oblong oval but they vary somewhat in shape as well as in size, some being more spherical than others. The majority measure 0·36 mm. by 0·29 mm. but they are sometimes as large as 0·37 mm. by 0·31 mm. or as small as 0·32 mm. by 0·3 mm. The first eggs laid by the newly mature female are of peculiar shape, being extremely elongated and pointed at both ends, measuring 0·46 mm. by 0·19 mm. When first laid the eggs are yellowish white but they change in two or three days through grey to black.

The Larva. (Plate XVI.)

The larva is legless, but the tenth segment forms a fleshy prominence which is used in walking and is capable of being extended or withdrawn. When full grown the larva measures about $6\frac{1}{2}$ mm. Its body is cylindrical in shape and tapers slightly towards the extremities. It is usually bent in a curve. It is creamy white in colour, soft and fleshy, and there are many transverse wrinkles on the back dividing the segments up into folds. These folds bear various reddish brown bristles which are constant in number and position in this species. The head is comparatively small, measuring 0·635 mm. long by 0·62 mm. broad. The frons and epicranium are deep ochreous in colour, becoming darker in colour towards the epistome which is reddish chestnut. The jaws are prominent, dark reddish brown. The antennae are extremely small, two jointed. There are no eyes. The body is divided into segments, of which there are three thoracic and ten abdominal, but the last abdominal segment is very small. Along the side of the body is a conspicuous longitudinal fold, the epipleural fold, above which the spiracles are situated. The spiracles are nine in number; the first pair is situated between the prothorax and the mesothorax, the remainder are situated on the abdominal segments 1 to 8.

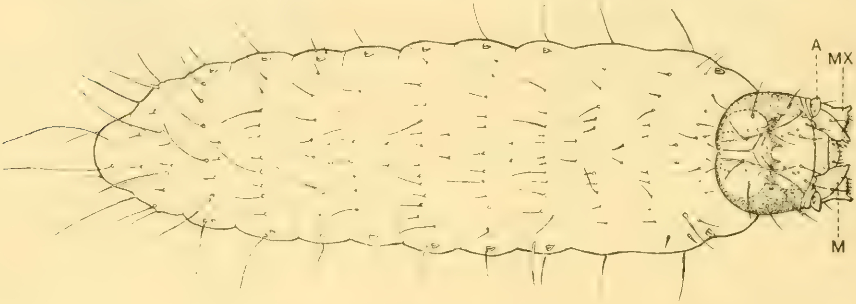
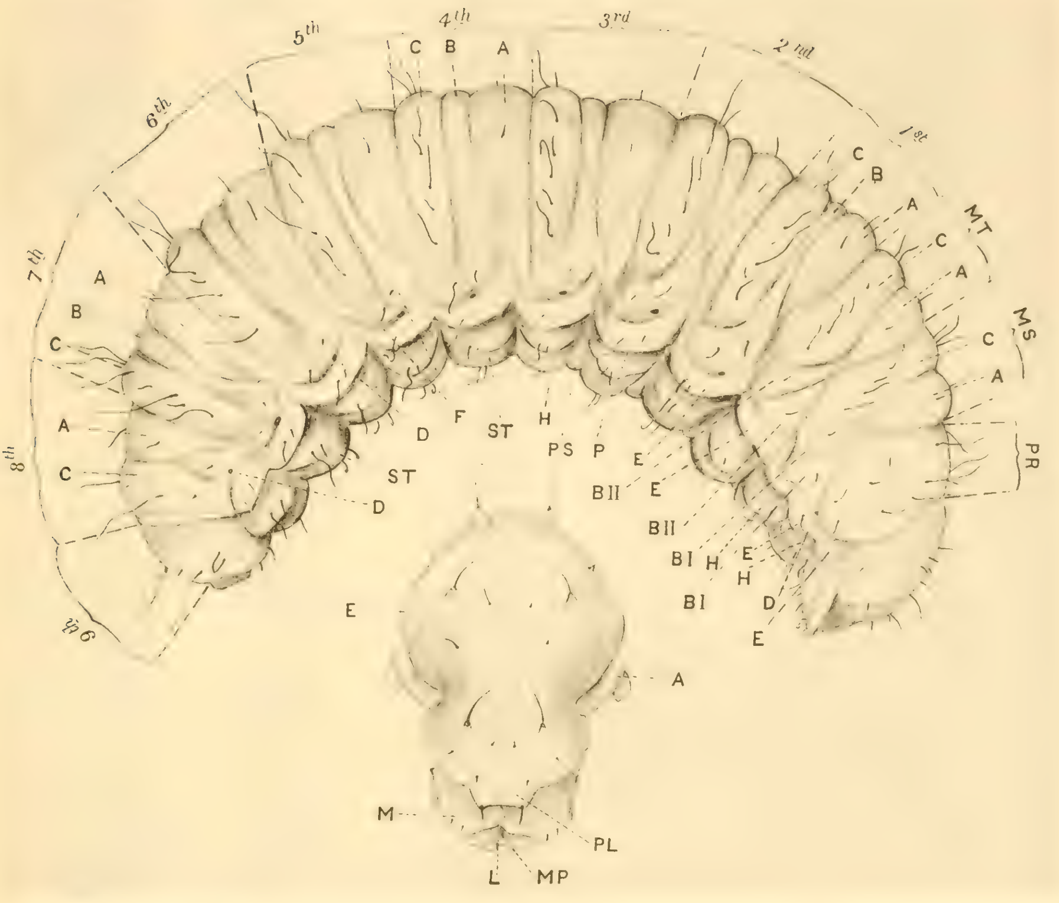


Fig. 3. Newly hatched larva of *Sitones lineatus* L. Dorsal view × 94.
A = antenna; M = mandible; MX = maxilla.

It is intended to give a more detailed description of this larva in a subsequent paper dealing with the comparative anatomy of the larvae of the injurious species.

The Newly Hatched Larva. (Fig. 3.)

The newly hatched larva differs from the adult larva in the following points. It is much more active and quick in its movements. Its bristles both on head and body are proportionately very much longer and increase greatly in length towards the end of the body. Their arrangement appears to be much the same as in the adult, but the lobes of the body on which they occur are not clearly represented. The spiracles are comparatively large and situated in the same position as in the adult. The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Adult larva of *Sitones lineatus* L., lateral view × 27½.

A = prescutal lobe; B = scutal lobe; B I = scutal lobe of mesothorax; B II = scutal lobe of metathorax; C = scutellar lobe; D = spiracle; E = epipleural lobe; F = basal portion of scutal fold; H = hypopleural fold; MS = mesothorax; MT = metathorax; P = pleural groove; PS = post sternellar fold; ST = sternellar fold; PR = prothorax; 1st to 9th = 1st to 9th abdominal segments.

Head of pupa of *Sitones lineatus* × 27½. (*Inset*)

A = basal portion of antenna; E = eye; L = labium; M = mandible; MP = maxillary palp; PL = pseudo-labrum or epistomal bristle pad.

head differs in colour from that of the adult. The sides of the epicranium and the genae or cheeks are dark brown, as is the gular plate. The frons and the dorsal part of the epicranium being colourless and transparent, these ventral parts appear conspicuously through the dorsal surface. The dark brown area is continued as a narrow strip round the posterior edge of the epicranium. The mandibles and epistome are very light ochreous brown. The antennae are relatively very much larger as compared with those of the adult larva. As in the adult, no eye spots are present. Measurements of the newly hatched larvae are as follows: length of body including head, 0·97 mm. to 1·1 mm.; breadth of body, 0·279 mm.; length of head, 0·182 mm. to 0·198 mm.; breadth of head, 0·163 mm. to 0·173 mm.

The Pupa. (Plate XVII. *Head of Pupa,* Plate XVI.)

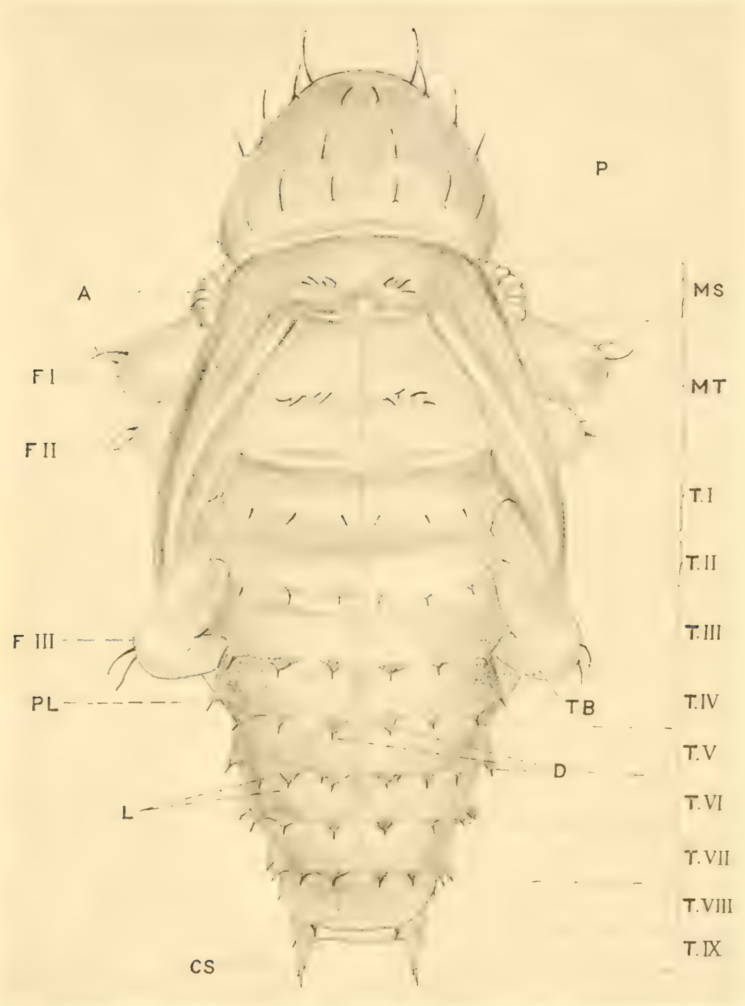
The pupa is soft, very easily crushed, creamy white in colour, with more or less conspicuous bristles upon the dorsal surface. It varies in length from under 4 mm. to over 5 mm. The head is bent beneath the prothorax and is therefore not visible when the pupa is viewed dorsally, only the two prominent bristles upon the vertex, and the distal portion of the antennae, curled round at the sides of the pronotum, being apparent. The head bears three pairs of prominent capitate bristles, each ending in a hooked point, the larger ones arising from distinct conical swellings, and some pairs of smaller bristles are also present. The pronotum is provided with a number of moderately long bristles of which the majority are non-capitate. The mesotergum bears on either side of the middle a group of four bristles, some of which are swollen at the tip. Occasionally there are two short bristles anterior to these groups situated one on each side of the median line. The metatergum bears a somewhat similar group of three to four bristles and has occasionally two bristles anterior to these as on the mesotergum. The bristles on the thoracic segments arise from slight elevations. There are ten abdominal segments, the tenth being extremely small and the first eight bear bristles which are arranged in the form of a single transverse row on the posterior portion of each segment. They are much shorter than the bristles of the thorax and slope towards the posterior extremity of the body. They are borne upon distinct paplike elevations, which become more marked on the posterior segments. The number of bristles upon the abdomen vary in different specimens but on segments 1–7 the number is usually eight, made up of one pair of dorsal bristles, two pairs of lateral bristles, and one pair of pleural bristles, but in some specimens there are six more smaller bristles on each segment, one occurring on each side between the dorsal and lateral bristles, another between the lateral bristles and one beside the pleural bristle. The eighth segment bears only one bristle-bearing pap on each side, the ninth terminates at each corner in a large and prominent spinous process which is covered especially posteriorly with numbers of minute pointed projections and bears on either side a backwardly directed spine. The tenth segment is visible on the ventral surface, between the spinous processes of the ninth segment. It consists of two lobes, representing tergite or supra-anal lobe and sternite or infra-anal lobe. The spiracles of the abdominal segments are situated on the sides in the region of the pleural bristles. The femora of the legs project prominently from the sides of the body, and each one bears at its extremity a pair of conspicuous hooked and capitate bristles.

EXTERNAL SEXUAL DIFFERENCES BETWEEN THE MALE AND FEMALE PUPAE.

The male and female pupae can be distinguished by examination of the posterior abdominal segments. The tergites, pleurites and sternites so clearly marked in the adult weevil can be traced in the pupae of both sexes as areas separated by ridges or incised lines. The abdominal tergites in the pupa comprise the region of the back occupied by the dorsal and lateral spines; the epipleural region containing the spiracles is indistinctly distinguished from the tergal region by an undulating ridge more conspicuous on the posterior segments. It bears dorsally the pleural spines. The hypopleurites can be easily recognised as flat areas on the sides below the epipleurites, and the ventral surface is occupied by the sternites. The external sexual differences are to be found in the shape of the seventh sternite and the eighth tergite.

The Male. (Fig. 4, A and B.)

The male pupa has the surface of the sternite of the seventh segment flat or only very slightly rounded; its outline when viewed from the side (Fig. 4, A) not projecting beyond the surface of the sternite of the eighth segment. The posterior edge of the seventh sternite where it meets the eighth sternite is almost quite straight and bluntly angulated at the junction of the hypopleurite of each side (Fig. 4, B). The tergite of the eighth segment is also longer and larger than in the female and its surface is flatter.


P
A
MS
F I
MT
F II
T. I
T. II
T. III
F III
PL
TB
T. IV
T. V
D
L
T. VI
T. VII
T. VIII
T. IX
CS

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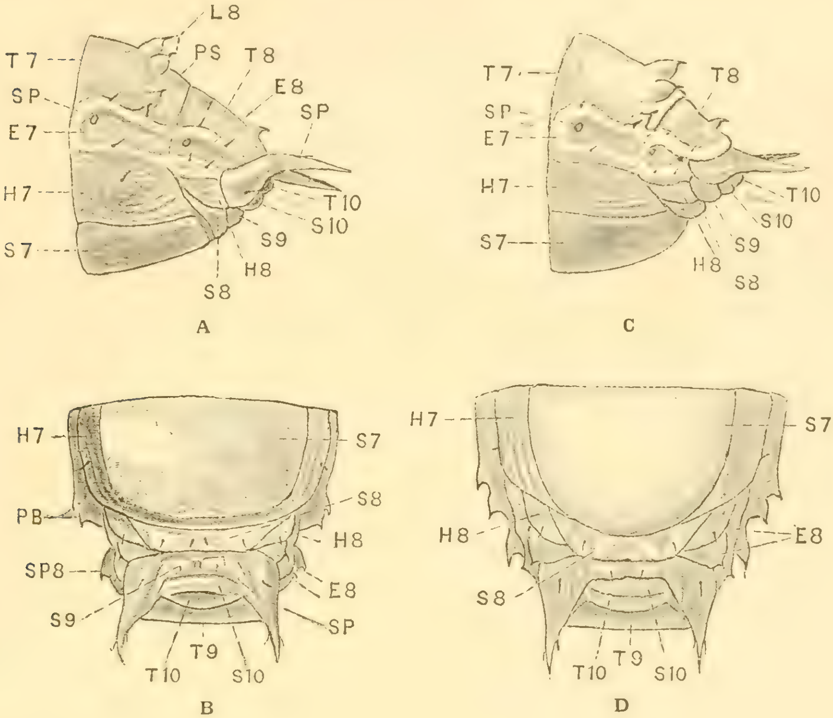
Pupa of *Sitones lineatus* L. Dorsal view × 27½.

A = antenna; CS = caudal spine; D = dorsal spines; F I = femur of 1st pair of legs; F II = femur of 2nd pair of legs; F III = femur of 3rd pair of legs; L = lateral spines; MS = mesotergum; MT = metatergum; P = pronotum; T. I–T. IX = 1st to 9th abdominal tergites; TB = tibia of 3rd pair of legs.

The Female. (Fig. 4, C and D.)

The female pupa has the surface of the sternite of the seventh segment more convex posteriorly than the male, so that its outline when viewed sideways is strongly curved posteriorly and projects prominently beyond the surface of the eighth sternite (Fig. 4, C). The posterior edge of the seventh sternite is also strongly and evenly rounded posteriorly (Fig. 4, D). The seventh tergite is much shorter than in the male with the surface less flat.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S8
T9
T10
S10
D

Del. D. J. Jackson

Fig. 4. Posterior abdominal segments of pupae of *Sitones lineatus* L. showing sexual differences × 35.

A. Male, lateral view.
B. Male, ventral view.
C. Female, lateral view.
D. Female, ventral view.

E = epipleurite; H = hypopleurite; L.S. = lateral spines; P.S. = pleural spines; S = sternite; S.P. = spinous process; T = tergite. 7, 8, 9 and 10 = 7th, 8th, 9th and 10th segments.

LIFE-HISTORY.

Summary of Life-History in Britain as at present known.

The most recent observations on the life-history of *S. lineatus* in Britain occur, as far as I have been able to discover, in Miss Ormerod's *Reports* from the year 1878 to 1892. They may be thus briefly summarised. Weevils of *S. lineatus* issuing from their winter quarters were known to attack peas and beans in spring. These beetles laid eggs, and larvae of this species were observed by Hart at the roots of peas in the end of May. Weevils emerged from these during July. Sitones weevils continued to be abundant on the peas until the time of harvesting, and in autumn adult Sitones were to be found in abundance amongst clover stubble. Sitones larvae were also to be found in great abundance at the roots of clover from November to May and adults emerged from these in June. As this observation is placed under the heading of *Sitones puncticollis* some at least of the weevils reared from these larvae must have been of this latter species.

Miss Ormerod's conclusions from these observations are that the weevils of *lineatus* after hibernation attack peas in spring, and produce there another generation which emerges in July; that in June the weevils developed from larvae which have spent the winter at the roots of clover, join the swarms on peas, and at the time of harvesting the peas all the weevils migrate to clover fields and a portion hibernate, but the remainder lay eggs which give rise to larvae that feed on clover roots throughout the winter.

From this one would understand that there is a partial second generation of the pea-feeding weevils at the roots of clover, but whether this generation is produced by the original hibernated weevils (in which case it would not be in the true sense a second generation but only a later brood of the same parents), or by their descendants, or by the weevils that emerge from clover in June, is left in doubt. My researches show that the life-history of two or more species have here been confused, as the larvae which occur at the roots of clover in winter are not those of *S. lineatus* but belong to other species, the life-history of which I intend to deal with in subsequent parts of this paper.

Summary of the Life-History as I have found it.

In the beginning of the year, from January until March or April, the adult weevils remain in their winter quarters, sheltering amongst long grass, in stacks of pea straw, amongst the stubble of clover fields, or even lying more or less exposed on the earth between the plants. In the first warm days of spring the majority migrate to peas and beans, only a very few remaining upon the clover. They very soon commence to lay eggs, and egg laying continues until shortly before the death of the parent weevil, in the south of England at the end of June or the beginning of July, and in the north of Scotland in August or the beginning of September. I have never observed the adults live through a second winter. The eggs hatch in 20 to 21 days and the young larvae become mature in about six or seven weeks. The pupal stage lasts about three weeks. The emergence of weevils is thus spread over several weeks commencing in England in July, in Scotland in August. All the weevils, however, emerge before the winter except in rare cases in the north of Scotland, when belated specimens are to be found in the pupal stage in mid-winter. The newly emerged weevils are sexually immature, the ovary of the female being quite undeveloped and maturing very slowly so that egg-laying does not commence till the following spring. The few weevils that remain upon clover throughout the summer oviposit similarly and their progeny develop in the same way, as I have proved experimentally. There is thus only one generation in the year.

DETAILED OBSERVATIONS ON LIFE-HISTORY AND HABITS.

As already mentioned the winter is passed in the adult stage. I will therefore commence to follow the life-history in detail from the time when the weevils make their appearance upon the peas and beans in spring, and will give an account of the field observation and breeding experiments upon which my conclusions rest. The field observations have been made at Wye, Kent, and in Ross-shire, and as differences occur in the time of appearance of the weevil in its different stages in these widely separated localities, I here record them. The breeding experiments have been carried out principally in Ross-shire. For this purpose flower pots were used in which the food-plant had been previously grown from seed, the pots being kept in a glasshouse to prevent the access of "wild" Sitones before the commencement of the experiments. A large wire ring was then attached horizontally to sticks thrust in the soil at the sides of the pot and the whole sleeved with muslin, the wire ring preventing the muslin from touching the leaves of the plants (Plate XVIII, fig. B). These pots were always kept out of doors and proved most useful for observing details of the life-history. With the object of carrying out control experiments under even more natural conditions, I had large breeding cages constructed 3 feet square with wooden sides about 1 foot high, and a frame above covered with muslin or finely perforated zinc. These cages were made without bottoms and the wooden sides were sunk in the earth, thus preventing any of the larvae from escaping and providing the plants with abundance of air and light. Admittance is obtained through sleeves let into the muslin, or, when perforated zinc is used, by a movable lid. In the photograph (Plate XIX) four of these cases are seen in position while the fifth is awaiting the process of digging in.

The hibernated weevils. The serious damage to peas and beans is done by the hibernated weevils in spring. The date of their appearance on these plants in spring varies according to the season and the latitude. In Kent, in 1918, the spring was normal, and I noted the weevils on the field peas for the first time on March 27th. In 1919 the season was very backward and I found no weevils until April 8th, and the majority did not appear till the middle of that month. In the north of Scotland, in 1919, the peas were not up till the beginning of May, and by the middle of that month weevils were abundant on them. Early in spring when the weather was cold the weevils were to be found in the daytime hiding under lumps of earth near the base of the plant, and sometimes on the stem of the plant near the root where it was sheltered by clods of earth, but in warm, sunny weather many of the weevils were to be found running about the leaves of the bean plants, or hiding in the leaf axils or between the unopened leaves. I noticed that their method of attack on the foliage of peas and beans differs after a certain stage. On beans the weevils feed principally on the young unopened leaves of the terminal shoots from the time the plant appears above ground till it is ready for cutting. With peas the terminal growing shoots are only eaten whilst the plant is small and not more than a few inches above the ground. When over a foot high the growing shoots are rarely touched and only the leaves near the ground are eaten. I attribute this difference to the greater shelter which the stiffer bean leaves afford to the weevils whilst eating. Large firm leaves, the axils of which form convenient hiding places, surround the young shoots of the broad bean, whilst on peas the young leaves are slenderer, more exposed, and the weevils have to seek shelter and a firmer foothold lower down. With both crops the most serious damage is done by the weevils early in the spring while the plants are still small. The weevils on disturbance immediately feign death and fall from the plant, but after a short pause run quickly under a clod of earth or down a crack, from which position they are not easy to secure. When present on peas or beans under natural conditions I have

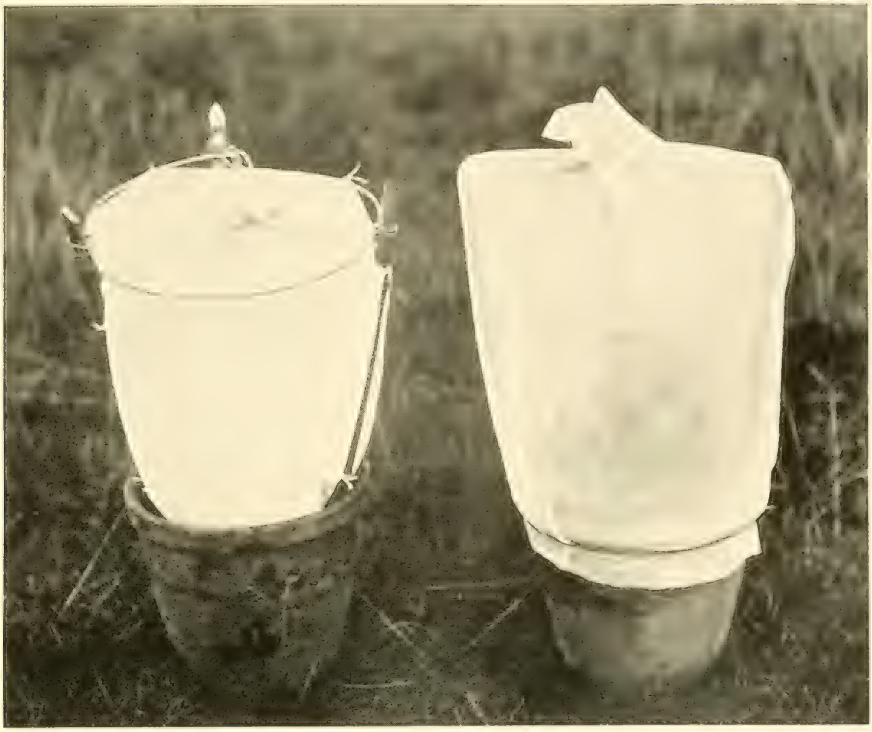

Fig. A. Fig. B.

PLATE XVIII

Fig. A. Pot containing growing clover, as used for observation of egg-laying of weevils, the thick muslin sleeve being fastened round the clover plants above the root.
Fig. B. Pot containing growing clover as used for breeding experiments.

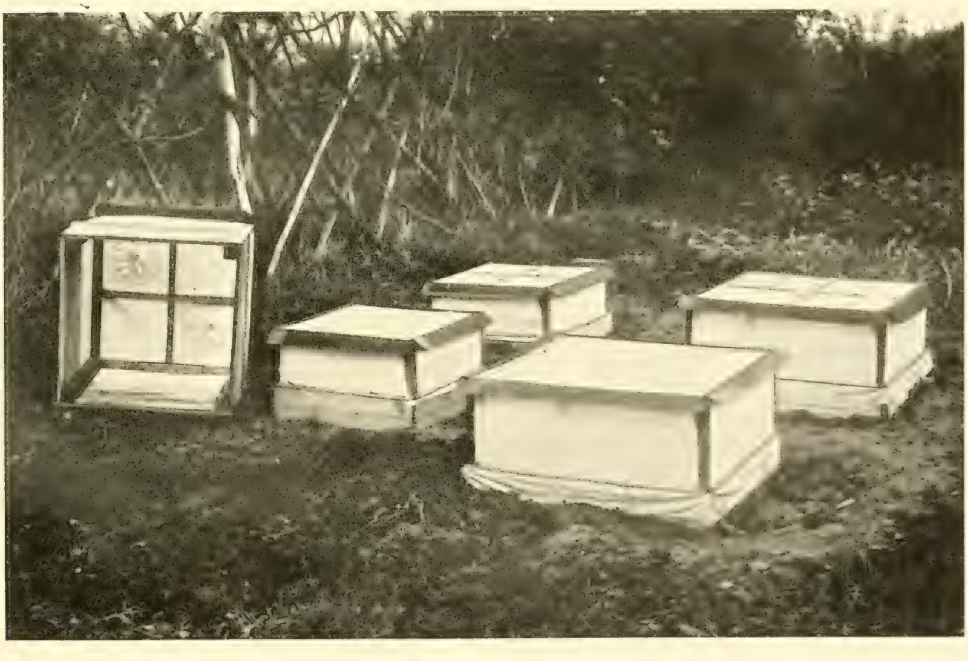

PLATE XIX

Cages used for breeding experiments.

never observed the weevils fly, but in spring if confined in a small space and placed in sunlight they become very active and use their wings freely. If liberated under these conditions they run about for a short time, then raise their elytra, spread their wings and fly quickly out of sight. The hibernated weevils were to be found in Kent until the beginning of July, and from Hampshire I received a hibernated female collected as late as August 11th. In Ross-shire they were to be found till the end of August or the beginning of September, but only a few occurred towards the end of these periods. As the weevils become older they get more rubbed till eventually practically all their scales disappear. They can thus be easily distinguished superficially from their newly-hatched progeny. In captivity weevils collected in Kent in April began to die off in the end of June, but a few survived till August 3rd. From weevils collected in Ross-shire in July a few survived in captivity till the middle of November. None of the hibernated weevils from Kent or Ross-shire were observed to live through a second winter.

Egg-laying. As will be shown later, the weevils do not commence to lay eggs until spring, but in the beginning of April in Kent, in the middle of May in Ross-shire, they lay eggs freely and are frequently to be found paired. At first only a few eggs, one to five, are laid per day, but later sometimes as many as 24 are laid daily. The numbers laid by different females varies greatly; thus one female under observation commenced laying on April 21st and continued laying till the beginning of September, producing in all 354 eggs, but another which commenced to oviposit on May 6th continued to do so till the middle of November, when a total of 1655 was attained. No doubt the confinement in small dishes which these experiments necessitated, together with the abundant food supplied, prolonged the life and the egg-laying activities of these weevils, as in fields even in Scotland egg-laying had ceased in September. A few days before commencement of egg-laying pairing takes place and continues throughout the egg-laying season. The eggs are laid indiscriminately amongst the earth at the base of the plant where the beetles rest, and whilst still pale in colour may often be seen adhering to the under-surface of the clods. The eggs shrivel up unless they are kept damp, but they hatch well if kept in moist earth.

The weevils continue to lay until a short time before their death but fewer eggs are laid towards the end and only a minority of these hatched. In confinement eggs laid at different dates throughout the summer hatched always in 20 or 21 days. The egg-laying period thus extends in

England from the beginning of April to the beginning of July, and in Scotland from the middle of May to the end of August.

The larval period. The young larva escapes from the egg by making an irregular hole at one end, and must then burrow to the roots of the plant, as on May 21st in a field in Kent, I found very young larvae measuring 1 mm. in length inside the nodules of the pea roots some distance below the surface of the ground. The larvae were to be found in a curved position inside the small nodules, but I failed to detect their presence from the external appearance of the nodule, and it was only by opening a large number with a needle that I found them. The larva must enter the nodule when newly hatched by a minute hole which is not easy to trace. I found several nodules with small holes in them but these were emptied of their contents and contained no larvae. When about quarter grown the larvae are to be found feeding freely upon the root nodules. On June 3rd larvae of different sizes were abundant at the roots of peas and beans in Kent, and one had already ensconced itself in an oval cell in the earth preparing for pupation. The larvae were always to be found amongst the root nodules, usually with their body partly buried in them. As many as six to nine larvae often occurred at the roots of a single plant in Kent and the nodules were much destroyed in consequence. By the middle of June in some pea fields in Kent, scarcely any nodules in a healthy condition were to be found on the roots, and the hollowed out ones that remained testified to the working of the larvae. In such cases no young larvae were to be found at the roots, so doubtless when a severe attack has already occurred many of the larvae resulting from later laid eggs will die from lack of food. In the north of Scotland larvae in various stages of growth were common at the roots of beans in the end of June, and full fed larvae were common on July 24th. Full grown larvae and even a few half-grown ones were still to be found in this locality on September 2nd, but the majority by this time were in the pupal stage.

Field observations would roughly indicate that the time taken for the growth of the larva from hatching till pupation does not exceed six or seven weeks, judging from the fact that in Kent the weevils commenced egg-laying in the beginning of April (the eggs taking three weeks to hatch), and the first pupa in the same locality was observed on June 10th. To determine the duration of the larval period more exactly, I carried out the following experiment in Scotland in one of the large breeding cages already described, in which peas had been grown from seed. I placed in this a large number of eggs laid between the 25th and

28th May. By July 23rd some of the resultant larvae were full grown and all were mature by July 31st. The first pupa was found on July 30th, and the remainder pupated between that date and August 6th. As the eggs would commence hatching from 15th to the 18th June this would give a larval period of from 45 to 49 days.

It is interesting to note that even when the species is bred in captivity under the most favourable conditions, only a few larvae survive from the many eggs originally used in the experiment, though sufficient food is present to support many more. As nearly all the eggs hatch when observed in the laboratory, no doubt the greatest mortality occurs amongst the newly hatched larvae (as pointed out by Baranov (17)), owing to lack of food whilst seeking for a root nodule to bore into. Greater difficulty was also experienced in breeding larvae on clover than on peas and beans.

The pupal period. The full fed larva excavates an oval cell in the soil for pupation ½ inch to 2 inches below the surface. In Kent I observed the first pupa on June 10th, and in Ross-shire on July 24th. In the latter locality pupae were abundant during August and still to be found in the beginning of September, whilst on January 17th I succeeded in finding two belated pupae in the soil of the old bean field. These must have resulted from the last laid eggs of the old weevils as the following breeding experiment testifies. On July 24th I placed some egg-laying females from Ross-shire on to a sleeved pot of clover, and on November 19th found a pupa in it which remained in this stage throughout the winter. All these belated pupae died in captivity. The pupal stage normally lasts from 16 to 19 days, but after casting the pupal skin the weevil remains in the earthen cell five or six days until the cuticle hardens and the normal colouring is assumed. About nine days before emergence colour changes may be observed in the pupa. The eyes first become brown, then the mouth parts and the apices of the femora and the tibiae darken, and before emergence the wing cases, face, antennae and legs are brownish grey. When the pupal skin is shed the weevil is entirely pale ochreous, with the head brownish grey, the eyes black and the apices of the femora and the entire tibiae deeper ochreous. The following day the thorax and legs become brownish grey and the elytra later turn greyish ochreous; by the fourth day the colour has become gradually darker, and on the fifth day the normal colour is usually assumed, though in some cases the cuticle is still soft.

The newly emerged weevils. These appear upon the peas and beans in July in Kent, in August in Ross-shire. From Suffolk Mr B. S. Harwood forwarded me a large number, all newly emerged, collected from beans on July 30th, but observed that earlier in the month no specimens of *lineatus* were obtainable. In captivity larvae collected from pea-roots in Kent on June 5th did not mature to weevils till the end of July and the beginning of August, but I have always found that collected larvae take longer to mature than those left undisturbed. In Ross-shire eggs laid from 25th to 28th May produced weevils towards the end of August. On emergence none of these weevils paired or laid eggs, and in order to see when they would do so under the most natural conditions possible I placed them in sleeves of muslin fastened tightly on to plants of peas or clover growing in pots (Plate XVIII, fig. A). These sleeves have proved very satisfactory, as the black eggs can be clearly seen upon them while they would be difficult to find if laid directly on the earth. The weevils also have plenty of fresh food and air. No eggs were laid by these specimens until the following spring, when on May 23rd the first female commenced oviposition. In the field I collected numbers of newly emerged weevils in Ross-shire in August and September, but none of these laid eggs until May 17th next year. In Kent, in October, I collected hundreds of weevils of *S. lineatus* and kept them under close observation, but not a single egg was laid by them that year. I placed a large number of these specimens on the sleeves described above and left them in Kent under the charge of Mr P. F. Kendall, who forwarded a sleeve to me each month, but none of these English weevils, even when kept in their own climate, laid any eggs until next spring when oviposition commenced on May 6th.

Conclusive proof that the weevils do not lay eggs the same year as they emerge will be shown in dealing with the reproductive organs.

On emergence the weevils commence to feed upon the peas and beans but do little harm as the plants by this time are full grown. When the crop is harvested the weevils mostly disperse and some are carted away with the crops, but a few are to be found in mid-winter on the old fields. I have taken these weevils abundantly on lucerne in Kent in October, also on clover and medick, and a few were present on bean plants that had grown up from fallen seed. In that month I also found numbers sheltering in a stack of pea straw and I took a few specimens again in this stack in the beginning of April. During the winter I have found the weevils sheltering amongst long grass beside which there was no clover. In captivity they thrive well with very little food during the winter. Thus in August I placed 15 specimens upon a pot of peas. The peas died during the winter and the weevils had no subsequent food, but on May 10th ten of the weevils were alive and active and commenced laying eggs on May 17th.

With the first warm days of spring the weevils leave their winter quarters and migrate to peas and beans and there commence their destructive work.

The length of life cycle of an average individual may be thus summarised: egg 3 weeks, larva 7 weeks, pupa 3 weeks, imago 12 months = Total 15 months.

The months during which the weevil occurs in its different stages in Scotland and England may be tabulated as follows:

	Kent	Ross-shire
Egg Stage	April and May diminishing June	May and June diminishing July
Larval stage	May to beginning July	End June and July diminishing August and September
Pupal stage	June and July	End July to September
Imaginal stage	July to July	August to August

THE REPRODUCTIVE ORGANS OF *SITONES LINEATUS*.

The reproductive organs of the newly emerged weevils are immature, particularly those of the female, which have to develop to four times their original size before egg-laying can take place. The male organs also undergo development but not to the same extent.

Description of the Reproductive Organs of the Mature Male. (Fig. 5, III.)

The male reproductive organs comprise testes, paired vasa deferentia, seminal vesicles, and seminal tubes, unpaired vas deferens or common duct and the internal sac. The latter has the appearance of being more or less surrounded by chitinous parts, consisting of tegmen and median lobe, which in reality form with the internal sac and connecting membranes a continuous tube inverted when not in use.

The *testes* are conspicuous yellow bodies lying one on each side of the body beneath the third, fourth, and fifth abdominal tergites. In their natural position the posterior part of the colon and rectum of the alimentary canal lie between the testes, but are dorsal to the vasa deferentia. Underneath the alimentary canal the struts of the median lobe project between the testes posteriorly. The testes of the mature male measure 1 mm. long by 0·85 mm. broad. Viewed dorsally the testes are oval and lobed in outline but are compressed dorso-ventrally (see Fig. 5, II, T). They are covered by a thin membrane which supports tracheae and strands of fat body, the latter imparting a yellow colour to the testes viewed as a whole.

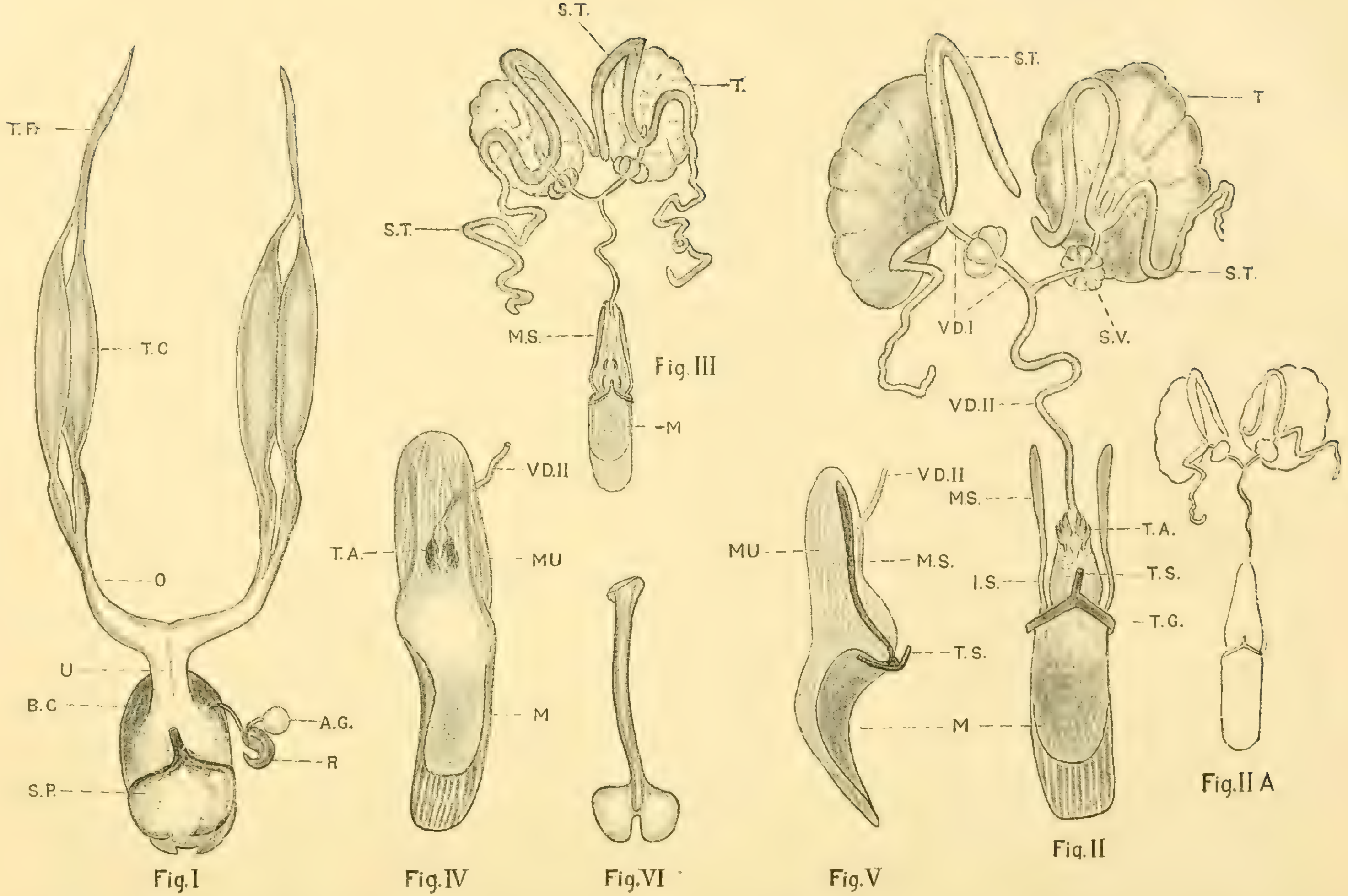
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Fig. III
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-M
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Fig.II A
Fig.II
Fig.I
Fig.IV
Fig.VI
Fig.V

Del. D. J. Jackson

Fig. 5. Reproductive organs of *Sitones lineatus* L. *For description of figure see opposite page.*

The paired *vasa deferentia* (Fig. 5, II, V.D.I) consist of a tube leading from the testes of each side to the unpaired vas deferens formed by their junction.

The *seminal tubes* (Fig. 5, II, S.T.) consist of two tubes on each side of the body which open into the paired vasa deferentia very close to the junction of the latter with the testes. These tubes are opaque white in colour and lie closely against the ventral surface of the testes. The inner tube is always more or less elbowed in shape and not convoluted; the outer seminal tube is very long in the mature male and greatly convoluted.

The *seminal vesicles* (Fig. 5, II, S.V.) are two in number, one being present on each side surrounding the paired vas deferens just below the junction of the seminal tubes. It is a transparent bulb-like structure consisting of eight lobes radiating from the centre. In the mature male they measure 0·34 mm. by 0·17 mm. long.

The *unpaired vas deferens* or common duct (Fig. 5, II, V.D. II) is formed by the junction of the paired vasa deferentia a short distance below the seminal vesicle. It is a long tube though when not extended during copulation it is coiled in a very short space. It opens posteriorly into the *internal sac*[1] (Fig. 5, II, I.S.), a membranous structure, the anterior part of which is covered with minute scales of chitin. At the junction of the vas deferens with the internal sac there is a chitinous structure known as the *transfer apparatus* (Fig. 5, II and IV, T.A.). In repose the internal sac is partially withdrawn inside the median lobe, its anterior end projecting between the struts of the median lobe, but when

I. Reproductive organs of immature female of *Sitones lineatus* L. from one to five months old × 37½, ventral view
II. Reproductive organs of immature male, ventral view, from one to five months old × 37½.
II A. Same but × 19½.
III. Reproductive organs of mature male eight months old as dissected in April × 19½.
IV. Male genitalia, dorsal view × 37½.
V. Same, lateral view.
VI. Spiculum gastrale of male × 37½.

A.G. = accessory gland; B.C. = Bursa copulatrix; I.S. = internal sac; M = median lobe; M.S. = struts of median lobe; M.U. = muscle; O = paired oviduct; R = receptaculum seminis; S.P. = spiculum ventrale; S.T. = seminal tubes; S.V. = seminal vesicle; T = testes; T.A. = transfer apparatus; T.C. = terminal chamber; T.F. = terminal filament; T.G. = tegmen; T.S. = tegminal strut; U = uterus; V.D. I = paired vasa deferentia; V.D. II = vas deferens.

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[1] The terminology of the genitalia which I here use is that adopted by Dr David Sharp, in his most valuable and helpful paper, "Studies in Rhynchophora," *Trans. of the Ent. Soc. of London*, Dec. 1918, pp. 209–222.

the genital tube is everted during copulation, the anterior end of the internal sac becomes the apex of the tube, and it is on this transfer apparatus that the functional orifice is situated.

The *median lobe* (Fig. 5, II, III, IV and V, M.) has the under-surface and sides chitinous and thus resembles a trough, the sides of which decrease in size towards the apex. It is of characteristic shape in the different species of Sitones which I have examined. It bears anteriorly two long chitinous struts which arise from its ventral surface with a pronounced angular curve. Between those struts and partly surrounding them is a mass of longitudinal muscles extending from the median lobe to the apex of the struts. These muscles encircle the apex of the internal sac and the transfer apparatus, and to examine these structures the genitalia have to be boiled in caustic soda to remove the muscles. The median lobe is protruded from the body during copulation but does not enter the genital tube of the female, the internal sac being everted through its apex. The median lobe measures 0·54 mm. long by 0·294 mm. broad, the struts 0·77 mm. long.

The *tegmen* (Fig. 5, II, T.G.), the chitinous part of the tegminal layer which forms the portion of the genital tube connecting with the apex of the abdomen, is represented by a semicircular band of chitin bearing anteriorly a short median strut. The median lobe when not functioning is drawn within the tegmen, so that the latter appears to be situated at its anterior edge on the ventral surface.

The *spiculum gastrale* (Fig. 5, VI) is a slightly curved chitinous rod which occurs beneath the genital tube at the apex of the abdomen. It is a median unpaired structure with the anterior end enlarged and the posterior end expanding into a spatulate disc. It measures 0·961 mm. long.

Development of the Reproductive Organs of Male.

The male of *Sitones lineatus* is mature nine months after emergence in the spring of the year following its emergence. The immature male (Fig. 5, II and II A) differs from the mature male (Fig. 5, III) in the following respects.

(1) The testes are smaller, measuring 0·8 mm. long by 0·6 mm. broad.

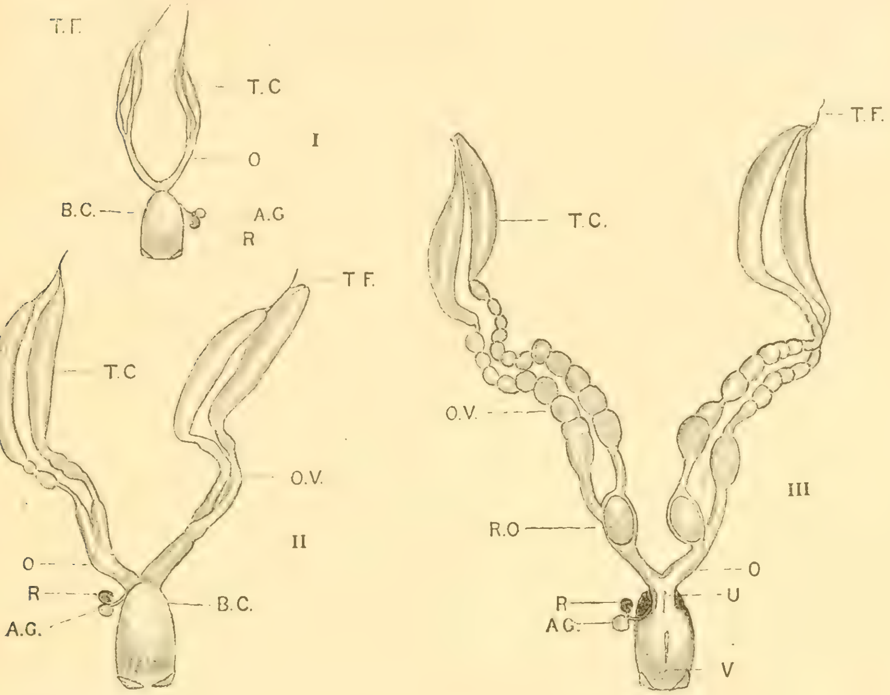
(2) The seminal vesicles are smaller, measuring 0·21 mm. broad by 0·13 mm. long.

(3) The seminal tubes are considerably smaller in size and breadth.

The other parts are the same as in the the mature male. The reproductive organs of the male weevil remain in this condition during the winter but growth commences about March.

Description of the Reproductive Organs of the Mature Female at commencement of Egg-laying. (Fig. 6, III.)

The mature reproductive organs in the female comprise the ovarian tubules, each with a terminal chamber; paired oviducts; unpaired oviduct or uterus; bursa copulatrix; receptaculum seminis and accessory gland. There are four *ovarian tubules* (Fig. 6, II and III, O.V.), two on each side of the body. Each is composed of a transparent tube enclosing



Del D. J. Jackson

Fig. 6. Reproductive organs of female of *Sitones lineatus* L. showing different stages in development × 15½.

I. Reproductive organs of immature female from one to five months old, as dissected from emergence of weevil in autumn until January, dorsal view.

II. Reproductive organs of older female—not yet mature—as dissected in March, dorsal view.

III. Reproductive organs of mature egg-laying female eight months old as dissected in April, ventral view.

A.G. = accessory gland; B.C. = bursa copulatrix; O. = paired oviduct; O.V. = ovarian tubules; R = receptaculum seminis; R.O. = ripe ovum about to be laid; T.C. = terminal chamber; T.F. = terminal filament; U = uterus; V = vagina.

a row of eggs of gradually increasing size; anteriorly the immature ova are small; but posteriorly, towards the junction of the two egg tubes with the paired oviduct of each side, full-sized mature ova occur. Anteriorly the egg tubes arise from an unsegmented portion called the *terminal chamber* (Fig. 6, I, II, III, T.C. and Fig. 5, I, T.C.). The ends of the two terminal chambers are united by means of the *terminal filament*. The paired oviducts unite after a short course to form the *unpaired oviduct* or *uterus* (U). On the dorsal side of the latter is a large sac, the *bursa copulatrix* (B.C.), which projects at its anterior edge from the uterus but elsewhere is united to it. The *receptaculum seminis* (R) is a small brown chitinous vesicle curved in the form of a hook and united by a slender tube to the uterus at the junction of the bursa copulatrix. A small white *accessory gland* (A.G.) is attached to the receptaculum seminis by a slender tube. The portion of the uterus below the bursa copulatrix is known as the *vagina*. At each side of it posteriorly is a small triangular chitinous plate, and before this on the ventral surface is a medium chitinous rod. A semi-transparent chitinous framework occurs in the ventral wall of the vagina. Attached by muscles to the ventral surface of the vagina is a large chitinous plate known as the *spiculum ventrale* (Fig. 5, I, S.P.).

Development of the Female Reproductive Organs.

On emergence from the pupa in autumn the reproductive organs of the female are exceedingly small and little developed. They remain in this state during the winter but growth commences in March, and by April or May the reproductive organs are mature and eggs are deposited. During spring and summer egg-laying is continued and the ovarian tubules continue to grow, increasing to about twice the size they were at the commencement of egg-laying, and to 12 times the size they were during the winter. Different stages in the growth have been selected, and are described below. Measurements are included to allow of comparison as to the growth of the different parts of the reproductive organs but on account of individual variation they can only be taken roughly.

Immature female, one to five months old (Fig. 6, I, and enlarged Fig. 5, I). In this stage all parts of the reproductive organs are extremely small, and the ovarian tubules show scarcely any development. The paired oviducts are proportionately long, and the terminal filament (arising from the terminal chamber) has attained its full growth. Measurements: ovarian tubule, 0·3 mm.; terminal chamber, 0·49 mm.; uterus and vagina, 0·6 mm.

Immature female, seven months old (Fig. 6, II). By this time considerable growth has taken place and the reproductive organs differ only from those of the female at the commencement of egg-laying in that the ovarian tubules are only one-third the size, and are unsegmented excepting for a small portion anteriorly. Measurements: ovarian tubule, 1·1 mm.; terminal chamber, 1·1 mm.; uterus and vagina, 1·0 mm.

Mature female at commencement of egg-laying (Fig. 6, III). This stage has already been described. Measurements: ovarian tubule, 3·3 mm.; terminal chamber, 1·3 mm.; uterus and vagina, 1·0 mm.

Mature female towards end of egg-laying. By this time the ovarian tubules have increased greatly in length whilst the other parts of the reproductive organs remain the same, the terminal chamber in some cases showing a slight decrease in size. About 20 segmented ova can be counted in each tubule, while the anterior portion of the ovarian tubule has become much attenuated and unsegmented. Measurements: ovarian tubule, 6·4 mm.; terminal chamber, 1·2 mm.; uterus and vagina, 1·0 mm.

THE LIFE-HISTORY OF *SITONES LINEATUS* AS OBSERVED IN FOREIGN COUNTRIES.

It is interesting to note that Molz and Schroder (18) consider *S. lineatus* as being double brooded in Germany, while in Denmark Rostrup (20) believes that this species has two generations in the year, the larvae of one generation overwintering, those of the other generation occurring in mid-summer. Kemner (21) only refers to one generation in the year of this species in Sweden, and Baranov (17) who gives a most interesting and detailed account of the life-history of *S. lineatus* in Russia, assumes that there is only one generation in the year, as the weevils which emerged in summer from eggs laid by the hibernated parents were not observed to pair the same summer.

NATURAL ENEMIES.

BIRDS.

Poultry eat these weevils readily. At the time of harvesting the peas and beans numbers of weevils are brought into the stackyard and many are then picked up by poultry. Miss Ormerod recorded that starlings occurred in numbers on pea fields infested by weevils.

PARASITES.

Ectoparasite. On August 4th I observed two specimens of *S. lineatus* each attacked by a mite which Mr S. Hirst has kindly examined for me. He thinks it probable that the mite—which is a larval form—belongs to the genus Trombidium or some closely allied genus. The mite occurred under the elytra of the beetle, lying upon the fourth to the seventh abdominal tergites, with its mouth-parts inserted in the body of the beetle between the junction of the fourth and fifth abdominal tergites. The mites were bright red in colour with pinkish legs and pale mouth-parts. One measured 0·93 mm. long by 0·49 mm. broad, the other 1·5 mm. long by 0·84 mm. broad. The weevils they were found upon had been collected from a bean field at Alness, Ross-shire, on August 2nd, and were both old males that had emerged the previous autumn. Neither seemed to be much the worse for the presence of the mite.

Endoparasites. (1) *Insectivorous.* I have bred a considerable number of the Braconid, *Perilitus rutilus* Nees from imagines of *Sitones lineatus.* I have found this parasite to occur on *S. lineatus* both in the south of England and in the north of Scotland. I am indebted to Mr G. T. Lyle for his identification of this and the following species, and to Mr K. G. Blair for passing on my inquiry to him. As I am at present engaged in the investigation of the life-history and habits of this parasite I hope to publish a complete account of it in a later paper. I have also bred a few specimens of two other species of Braconidae from imagines of *S. lineatus* collected in Suffolk by Mr B. S. Harwood. These are *Pygostolus falcatus* Nees, the fuscous variety described by Ruthe, and *Liophron muricatus* Hal, var. *nigra*. Both appear to be rarer parasites of *S. lineatus* than is *Perilitus rutilus* Nees.

(2) *Fungoid.* The most effective parasite of *S. lineatus* that I have yet observed is a fungus *Botrytis bassiana* (Balsamo) Montagne, the Muscardine of silkworms, which has been identified for me through the kindness of Mr A. D. Cotton and Mr R. Beer at the Mycological Laboratory, Kew. This fungus is particularly common upon weevils of Sitones kept under artificial conditions, but I have also observed specimens of *S. lineatus* attacked by it in the field. It is always fatal to the weevil attacked. While most easily observed upon the adult, I have proved experimentally that it also causes death to the pupae and to the larvae in all stages of development. Many experiments have already been carried out on infecting the weevil with spores of the fungus both in the laboratory and under muslin sleeves out of doors, all of which have

proved successful, death occurring nine to thirteen days after infection. It is therefore intended to continue this work on a larger scale and to record the results later.

In conclusion my thanks are due to Mr F. V. Theobald for encouraging me to undertake this research, and to Dr R. Stewart MacDougall for valuable help and advice in its prosecution and for the reading of this paper. I am also indebted to Mr H. Britten for identifying the weevils for me, to Miss L. H. Huie for much valuable advice in technique and other matters, to Mr P. F. Kendall for assistance in carrying out parallel breeding experiments at Wye, and to Dr W. Ritchie for valuable hints in making preparation of my dissections.

As I am at present engaged in the investigation of the life-history and habits of *Sitones puncticollis*, *flavescens*, *hispidulus*, *humeralis*, *sulcifrons*, and *crinitus*, I should be extremely grateful if any interested in the subject would forward me specimens of any of these species found injuring leguminous crops, together with full particulars.

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THE STRUCTURE, BIONOMICS, AND ECONOMIC IMPORTANCE OF *SAPERDA CARCHARIAS* LINN., "THE LARGE POPLAR LONGHORN."

By WALTER RITCHIE, B.Sc., B.Sc. (Agr.),

Carnegie Research Fellow, University of Edinburgh.

(With Plates XX–XXIII and 25 Text-figs.)

The assurance that a definite scheme of afforestation is to be established in Britain has given a fresh stimulus to the study of insects injurious to our forest trees. Already observations on the life histories and habits of such forms have been called for, as without a knowledge of these, no definite measures of control whether preventive or remedial can be undertaken.

The following intensive research on the structure, habits and life history of *Saperda carcharias* Linn. the "Large Poplar Longhorn" is therefore opportune, for to forester and nurseryman the species is of primary importance as it may prove to be very destructive to healthy young poplars.

In the adult stage the Large Poplar Longhorn causes some injury by feeding upon the leaves and by ovipositing in the basal portions of the stems, but the greatest amount of damage is done by this insect, while in the larval state, for by the larvae feeding and boring in the stems, and occasionally tunnelling into side branches, healthy trees are very soon killed or rendered worthless.

The genus Saperda (Fabricus), to which our species belongs, contains about fifty species, but of these only eight are European. In Britain only three species are found, viz.: *Saperda carcharias* L., *S. scalaris* L., and *S. populnea* L. Of these only the two first named have been found in Scotland, and as far as we know, only *S. carcharias* and *S. populnea* are of economic importance, the third species being known mostly to Coleopterists and highly prized by them on account of its handsome colouration.

In England, *S. carcharias* is a fairly well known beetle, but in Scotland, it is little known, its occurrence according to Fowler (1)[1] being very rare. However, in certain areas in the neighbourhood of Aboyne, Aberdeenshire, I have found this species present in large numbers doing great damage among the young poplars of natural growth. In gardens, too, in the village of Aboyne where poplars have been planted for ornamental purposes, these have been completely destroyed through the repeated attacks of *S. carcharias*.

It was in these areas that the study of the life history of the insect was carried out by experiment and field observations, while the anatomical and microscopical studies and some breeding experiments were undertaken in Dr Stewart MacDougall's laboratory in Edinburgh University.

CHARACTERS OF THE GENUS SAPERDA.

The genus Saperda is singled out by Fowler (2) from the other Lamiidae, the sub-family to which it belongs, by the following characters—

Femora not or scarcely clavate.
Thorax without lateral spines.
Tarsal claws simple.
Anterior coxae distant.
Antennae ringed with white.
Mesosternum not protuberant between intermediate coxae.
Form elongate.
Antennae eleven jointed.

In view of the work of Gahan (3) and Felt (4) this key of Fowler's, in which he places the genus Saperda under the forms with simple claws, requires modification.

Those two workers point out that, although simple claws are present in some species, *e.g. Saperda populnea*, others possess bifid claws. In the species which possess bifid or compound claws these are confined to the male sex. The bifid claws sometimes are found in the first two pairs of legs as in *Saperda carcharias*, sometimes only in the first pair of legs and sometimes only in the second pair of legs. According to Le Conte, who was the first worker to draw attention to the presence of these claws in the genus Saperda, it is only the inner or anterior claw of the tarsus that is toothed, or bifid.

The following is Fowler's (1) description of *Saperda carcharias* adult:

> One of the largest and most conspicuous British Longicorns, black, clothed with yellowish or ashy-grey pubescence which is thicker and longer on the under surface

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[1] The numbers in brackets refer to the "Literature," p. 342.

than on the upper, and is somewhat variable in colour, so that the insect appears to vary from quite a lighter grey to an ochreous-yellow; head large, antennae tapering with the apical joints not ringed with white; thorax slightly transverse, coarsely and rugosely punctured, with a central line and a tubercle on each side of it which are usually covered with pubescence; scutellum large, semicircular, elytra broad, with well marked shoulders, gradually narrowed at apex, which terminate at suture in a short blunt spine, very coarsely and deeply punctured, with a transverse patch of closer pubescence on each about the middle; legs short and stout, pubescent, extreme apex of femora usually black. L. 20–28 mm.

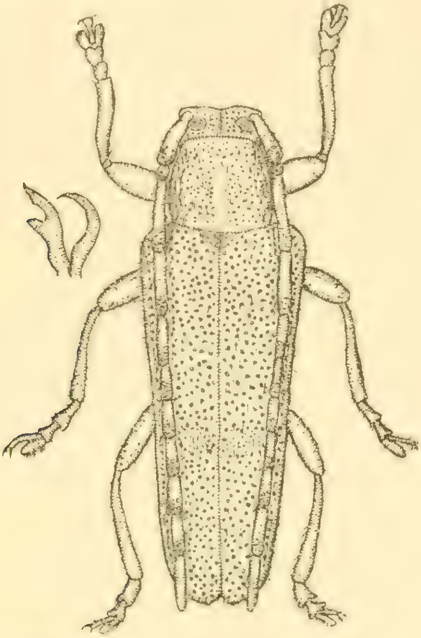

Fig. 1. The large poplar Longhorn, *Saperda carcharias* L. Male. Tarsal claws of a foreleg are shown on the left (both greatly magnified).

Male (Fig. 1) with antennae a little longer than the body, and the elytra more narrowed behind; female (Fig. 2) with the antennae a little shorter than the body, the elytra slightly narrowed behind and the fifth ventral segment of the abdomen with a fine channel towards base.

SEXUAL DIFFERENTIATION IN *S. CARCHARIAS.*

From my observations made in handling a very large number of individuals of both sexes, I find there is no difficulty in differentiating them, for not only are they different in size but they also differ in their general form; there is the difference also in the tarsal claws to which I have already referred.

A further distinguishing sex character, noticeable in the majority of my northern specimens is that of colour. The majority of the males are dark ash-grey, while all the females are greenish-yellow. Later in this work I refer to this difference in colour between the sexes.

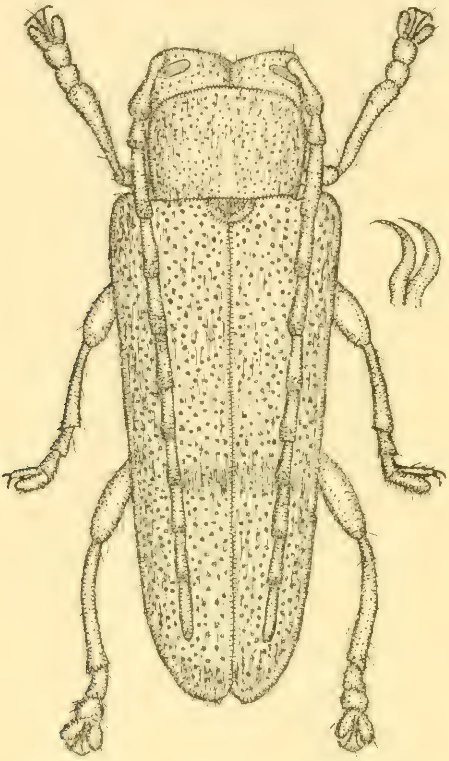

Fig. 2. The large poplar Longhorn, *S. carcharias* L. Female. Tarsal claws of a leg are shown on the right (both greatly magnified).

The principal external differences in the sexes may be thus contrasted:

	Male (see Fig. 1)	Female (see Fig. 2)
Size	18 mm.–22·5 mm.	24·5 mm.–27·5 mm.
Length of antennae ...	Longer than body	Shorter than body
Shape of prothorax ...	Quadrate	Broader than long
Tarsal claws of 1st and 2nd pairs of legs ...	One claw bifid or toothed	Simple
Breadth of elytra at base	7 mm.–7·5 mm.	8·5 mm.–9·5 mm.
Shape of elytra ...	Outer margins taper markedly towards apices	Outer margins taper less markedly towards apices
Shape of abdomen ...	Thin; groove on 5th sternite absent	Stout; groove on 5th sternite present and conspicuous

Egg of S. carcharias.

The egg when newly laid is elongate, rounded at the ends and oval in section. Its length ranges from 3·5 mm. to 4·1 mm., and it measures from 1·5 mm. to 1·8 mm. at its greatest breadth. The shell is very tough. being almost leathery in texture, has a smooth surface, and is dull yellow in colour. In general, its colour resembles very much that of the bast or outer wood in which it is deposited. It is not uncommon to find in eggs which have been laid for some time, that as a result of the pressure to which they are subjected, their shells have taken the pattern of the grain of the fibres with which they are in contact. So closely does the colour of the newly laid egg harmonise with that of the tissue in which the egg is deposited, that on several occasions in my first attempts to expose the eggs to view by carefully tearing away the outer bast layers, my eye was so deceived that the eggs were accidentally destroyed.

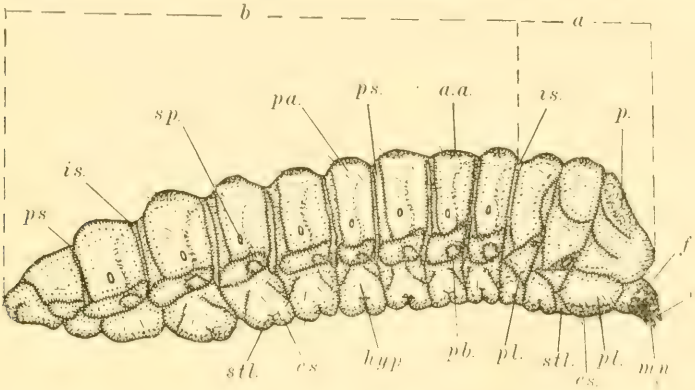

Fig. 3. Larva of *S. carcharias*, side view (greatly magnified). *a*=thorax; *aa*=ambulatory ampulla; *b*=abdomen; *es*=eusternum; *f*=frons; *hyp*=hypopleurum; *is*=intersegmental skin; *l*=labrum; *mn*=mandible; *p*=pronotum; *pa*=parascutal area; *pb*=pleural band; *pl*=pleural lobe; *ps*=postscutellum; *sp*=spiracle; *stl*=sternellum

In the case of over-wintered eggs the colour of the shell is dark brown and the egg itself is much swollen, in fact such eggs look like small Dipterous puparia.

As compared with eggs found *in situ*, those dissected out of an egg-laying female are somewhat different in shape and different in colour; they are elongate-oval, circular in section and pure white in colour.

Larva of S. carcharias (Fig. 3).

The larva of *S. carcharias* is a typical Lamiid larva and is extremely well adapted to its mode of life. It is a soft, fleshy, legless grub. elongate in form, and almost cylindrical in section. It varies in length from 4·5 mm. when newly hatched, to about 37·5 mm. or over when fully grown.

It is broadest across the first thoracic segment, and gradually tapers towards the tip of the abdomen. The body is deeply wrinkled and is covered with fine scattered hairs.

The larva is made up of the chitinous head-piece and thirteen segments, the first three of these forming the thorax, the remaining ten the abdomen.

The head portion is highly chitinised and posteriorly is deeply sunk in the first thoracic segment.

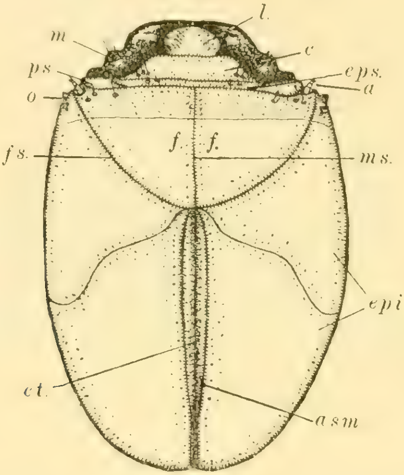

Fig. 4. Head of larva, *S. carcharias*, seen from above (greatly magnified). *a*=antenna; *asm*=attachment area of the superior retractor muscles of the head; *c*=clypeus; *epi*=epicranium; *eps*=epistome; *et*=epicranial suture; *f*=frons; *fs*=frontal suture; *l*=labrum; *m*=mandible; *ms*=median suture; *o*=ocellus; *ps*=pleurostome.

The thoracic segments are somewhat larger than the abdominal ones. The eighth and ninth abdominal segments taper posteriorly and are smaller than the others, while the last or tenth segment is made up of three lobes surrounding the anus.

There are ten pairs of spiracles, the first pair being the largest. The first pair of spiracles lie in a hollow between the first and second thoracic segments. The second pair, which are very small, are present on the third thoracic segment while the other pairs are borne by the first eight abdominal segments. Each spiracle is oval in shape and is surrounded by a chitinous ring.

The Head (Fig. 4).

If the head of the larva be dissected out from the first thoracic segment and examined under the binocular microscope, the following parts are seen: in the centre of the field is the triangular region of the frons (*f*), bounded on each side by the frontal suture (*fs*), and divided into two by the median suture (*ms*).

At the base of the triangular frons is a narrow area, the epistome (*eps*), on each side of which is a very highly chitinised area, the pleurostome (*ps*). Anterior to the epistome is the clypeus (*c*), trapezoidal in shape and bearing a few bristles on the sides; attached to the clypeus anteriorly is the bristly labrum (*l*) which is almost semicircular in shape.

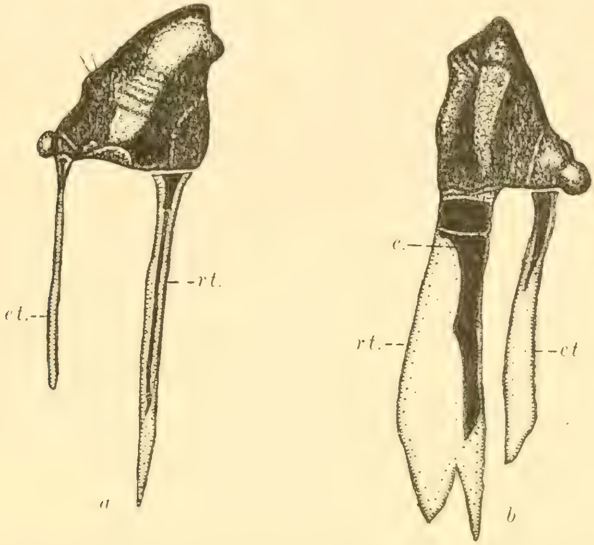

Fig. 5. Left mandible of larva, *S. carcharias* (greatly magnified). *a* = dorso-lateral view of mandible; *b* = ventral view of mandible; *c* = chitinous plate; *et* = extensor muscle; *rt* = retractor muscle.

On each side of the clypeus and labrum can be seen, in part, the mandibles (*m*). Each mandible (see Fig. 5) is strong and robust, shiny-black in colour and highly chitinised. Their general form is triangular and their inner cutting edges are produced into two blunt teeth. Each mandible is worked by two powerful muscles, an extensor (*et*) attached to the dorso-lateral surface of the mandible and a retractor (*rt*) to its inner or ventral surface. The retractor muscle is far the stronger of the two. Embedded in each muscle is a thin sheet of chitin (*c*).

Between the pleurostome (Fig. 4, *ps*) and the anterior angles of the frons (*f*), the antennae (*a*) are placed. Each antenna is sunk in a hollow and is five-jointed; alongside the small fourth joint of the antenna and external to it is the fifth joint, the smallest of all.

On each side of the frons (*f*), to the outside of the antenna (*a*) and somewhat posterior to the latter, is situated an ocellus (*o*). The ocelli have the appearance of minute knobs or nodules.

In Fig. 6 the view of the epistomal region is much enlarged and the various details will be more clearly understood by referring to it.

Looking now at the parts of the head posterior to the frontal suture (*fs*, Fig. 4), one can make out the epicranium (*epi*) divided into two by the epicranial suture (*et*), and lying in a groove (*asm*), the latter forming the attachment area of the superior retractor muscles of the head.

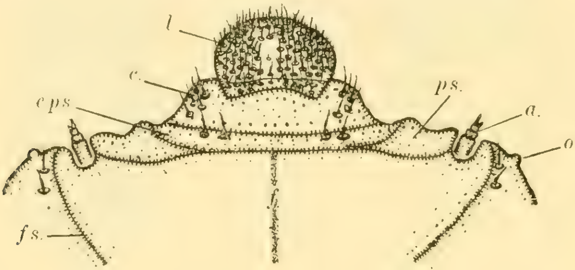

Fig. 6. Region of epistome, *S. carcharias* larva (very highly magnified). *a*=antenna; *c*=clypeus; *eps*=epistome; *f*=frons; *fs*=frontal suture; *l*=labrum; *o*=ocellus; *ps*=pleurostome.

From the apex or posterior angle of the frons (*f*) a curved marking may be observed to run across the epicranium. This marking forms the anterior boundary of the portion of the head sunk in the first thoracic segment.

Looking now at the head ventrally (Fig. 10, *b*) one can distinguish anteriorly the maxillae.

Examining these parts in detail (Fig. 7), on each side (the outermost parts in this view) lies the 1st maxilla, composed of five portions; the cardo (*c*); next the stipes (*st*) bearing a few chitinous bristles and with its posterior portion strengthened by a band of thicker chitin; the maxillary palpifer (*mxp*) which bears a three-jointed maxillary palp (*mp*) to the outside and the lacinia (*la*) to the inside, the latter covered with stiff bristles.

In the centre of the field lie the fused 2nd maxillae or labium. This region of the mouth parts is made up of the mentum (*m*) and the labial palpifer (*lf*) with a few bristles; this palpifer carries the two-jointed labial palps (*lp*) and the ligula (*l*) densely covered with bristles. The submentum (*sm*) is posterior to the mentum, while surrounded by these two portions and by the cardo (*c*) and stipes (*st*) is an area somewhat circular in shape, the maxillary sclerite (*mxs*); the exact demarcation lines of this last named portion are in most cases difficult to make out.

If the mandibles and ventral mouth parts described above be removed and the under surface of the head (Fig. 8) examined, one can make out in the centre a large opening, the occipital foramen (*of*) through which may be seen the head muscles (*hm*); between this foramen and the maxillary foramen (*mf*), now clear to view, lies the region called the gula (*g*); its lateral sutures diverge posteriorly and meet the tentorial region (*t*); beside the gula, on each side, lies the hypostome (*hs*) with its external suture convex.

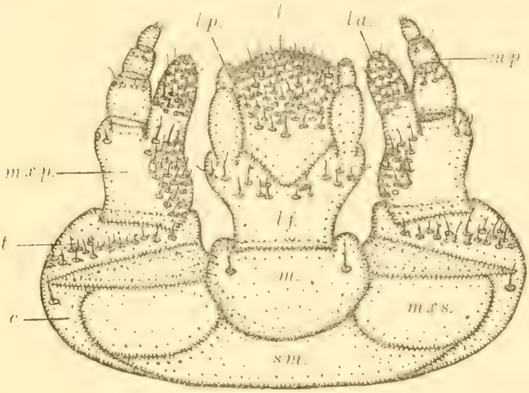

Fig. 7. Maxillae and labium of *S. carcharias* larva (greatly magnified). *c*=cardo; *l*=ligula; *la*=lacinia; *lf*=labial palpifer; *lp*=labial palp; *m*=mentum, *mp*=maxillary palp; *mxp*=maxillary palpifer; *mxs*=maxillary sclerite; *sm*=submentum; *st*=stipes.

Other portions seen in this view of the head, already referred to in describing the dorsal view, are the pleurostome (*ps*), lying on the lateral margin of the maxillary foramen (*mf*); the clypeus (*c*), the labrum (*l*), attached to which are two strands of chitin called the labral hooks (*lh*), the ocelli (*o*) and the ventral portion of the epicranium (*epi*).

The Thorax (Fig. 3, *a*).

In side view, immediately following the chitinous head piece we have the prothoracic, the mesothoracic and the metathoracic segments. Of these three segments the prothoracic is far the largest, being nearly equal in size to the other two taken together. Besides differing in size, the prothoracic segment differs considerably in structure from the other two thoracic segments.

Viewed from the side the prothorax shows the following regions: dorsally the large pronotum (*p*), laterally the pleural lobe (*pl*), and ventrally the eusternum (*es*)[1] and the sternellum (*stl*). The mesothoracic and the metathoracic show, in side view, the mesonotum and metanotum respectively on their dorsal surface, the pleural lobe medially, and the eusternum (*es*) and sternellum (*stl*) ventrally (see Fig. 10, *b*). Ventral to the pleural lobe and lying between it and the eusternum and sternellum, is the hypopleurum (*hyp*). Situated in a cavity between the prothorax and the mesothorax is the large thoracic spiracle, while on the metathorax lies the small spiracle.

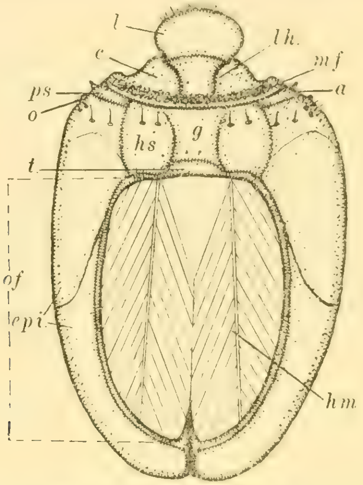

Fig. 8. Head of larva of *S. carcharias*, seen from below; the maxillae, labium, and mandibles removed (greatly magnified). *a* = antenna; *c* = clypeus; *epi* = epicranium; *g* = gular plate or gula; *hm* = muscles in head; *hs* = hypostome; *l* = labrum; *lh* = labral hooks; *mf* = maxillary foramen; *o* = ocellus; *of* = occipital foramen; *ps* = pleurostome; *t* = tentorium.

The Abdomen (Fig. 3, *b*).

The first seven abdominal segments are similar in structure to each other and show the following regions: the swollen parascutal lobe (*pa*) and the postscutellum (*ps*) dorsally (described more fully below); the pleural zone or lobe medially; the hypopleurum (*hyp*), eusternum (*es*), and sternellum (*stl*) ventrally.

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[1] The terminology used in this description of the larva is that adopted by F. C. Craighead in *Report No. 107, U.S. Dept. of Agriculture*, 1915. "The Larvae of the Prioninae." See also, *A Preliminary Synopsis of Cerambycoid Larvae*, by J. L. Webb, Tech. Series, No. 20, Part V, Bureau of Entomology, U.S. Dept. of Agriculture, 1912.

Dorsal to the pleural zone on each segment a spiracle (*sp*) is situated. On each of the pleural folds there is a swollen band (*pb*) bearing fine hairs.

The eighth body segment, in side view, has a similar appearance to the first seven, only no parascutal, hypopleural, eusternal, or sternellar lobes are present.

The ninth segment is similar to the eighth, only it lacks spiracles and shows no postscutal area.

The tenth abdominal segment is divided by three deep sutures into three lobes—one dorsal and two latero-ventral—which surround the anus.

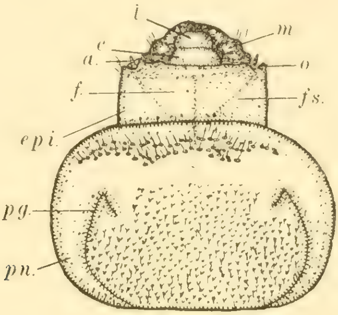
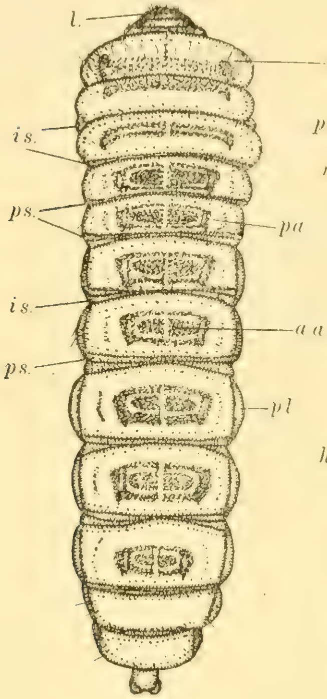


Fig. 9. Dorsal surface of first thoracic segment of larva, *S. carcharias*. Head also shown here in natural position (both parts greatly magnified). *a*=antenna; *c*=clypeus; *epi*=epicranium; *f*=frons; *fs*=frontal suture; *l*=labrum; *m*=mandible; *o*=ocellus; *pg*=pronotal groove; *pn*=pronotum.

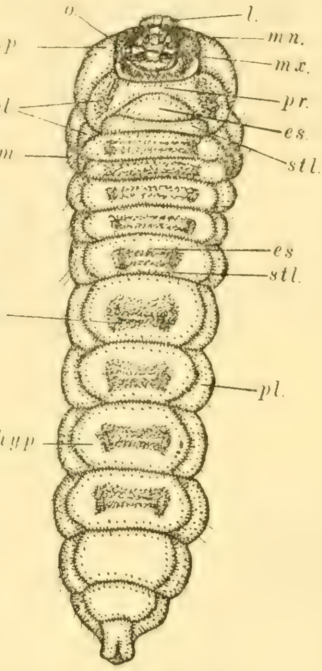
Between the segments are bands of intersegmental skin (*is*). This allows free longitudinal expansion and contraction of the segments. This skin is more marked between some of the segments of the body than between others.

Looking now at the larva dorsally, one can see clearly the large pronotum (Fig. 10 *a*, *p*) lying immediately behind the head. In the enlarged view of this region (Fig. 9) the pronotum (*pn*) is seen to bear on each side a curved groove (*pg*), running anteriorly and then sharply bending backwards for a short distance. Between these two grooves there are numerous chitinous asperities, while running transversely along the anterior margin of the pronotum is a row of chitinous bristles. The dorsal area of the second thoracic segment—the mesonotum—shows a transverse row of very short stiff bristles along its anterior margin, while that of the metanotum shows a double row of similar bristles with a depression between them.

The dorsal areas of the first seven abdominal segments resemble each other in appearance; they have fleshy protuberances which show two transverse depressions and bear short, stiff bristles. These bristles are arranged as in Fig. 10 *a*, and the areas which bear them are known as the ambulatory ampullae (*aa*).



(*a*)



(*b*)

Fig. 10 *a*. Larva of *S. carcharias*, dorsal view (greatly magnified). *aa* = ambulatory ampulla; *is* = intersegmental skin; *p* = pronotum; *pa* = parascutal area; *pl* = pleural lobe; *ps* = postscutellum.

Fig. 10 *b*. Larva of *S. carcharias*, ventral view (greatly magnified). *es* = eusternum; *hyp* = hypopleurum; *l* = labrum; *m* = metanotum; *mn* = mandible; *mx* = maxillae; *o* = ocellus; *p* = pronotum; *pl* = pleural lobe; *pr* = presternum; *stl* = sternellum.

Surrounding each ampulla is an elliptical area, slightly swollen laterally, called the parascutal lobe (*pa*). Behind the ampulla on each segment is the postscutellum (*ps*). The eighth segment resembles the previous segment but has no ampulla and therefore no parascutal area. The ninth is similar to the eighth only it shows no postscutellar area. The tenth segment has the dorsal lobe rounded in shape above, and the ventral lobes projecting in part from below it. In all the thoracic and abdominal segments except the tenth abdominal, the pleural fold or lobe (*pl*) is seen projecting on each side of the larva.

Now laying the larva on its dorsal surface so as to view it from the ventral side, the first thoracic segment (Fig. 10 *b*) shows three regions or folds, the presternum (*pr*), the eusternum (*es*), triangular in shape, and the sternellum (*stl*), almost rectangular in form.

On the mesothoracic and metathoracic segments, in ventral view, may be seen a thick row of short stiff bristles divided transversely by a depression into two folds, the anterior of which is the eusternum (*es*), and the posterior, the sternellum (*stl*).

The first seven abdominal segments resemble each other in appearance. Their sternal areas are developed into fleshy protuberances, the ambulatory ampullae (*aa*) carrying short stiff bristles (Fig. 10 *b*). The sternal ampullae however show only one transverse depression. Each ampulla is surrounded by a swollen area called the hypopleurum (*hyp*).

The eighth and ninth segments show no ampullae and hence no hypopleura; the tenth shows the two latero-ventral lobes. In all the body segments except the last the pleural lobe (*pl*) is seen projecting laterally; in the first thoracic segment this area may be easily picked out by its reddish-yellow colour.

The Pupa.

The pupa (Figs. 11–13) at first is shiny-white in colour. As development progresses, a darker colour is first noticeable in the eyes and mandibles. Later, the whole of the body takes on the colour of the adult insect. The size varies slightly in the sexes and in different specimens of the same sex. In length, the male is on an average 24 mm. while the average breadth at base of the elytra is about 7·5 mm. In the female, the average length is 26 mm. while in breadth it measures 9 mm. The head has the same general appearance as that of the adult, only it is bent underneath the body so that the mouth parts point backwards.

In a side view of the pupa (Fig. 11) the various appendages of the body are visible. The antennae (*a*) arise on the side of the head in front of the eyes (*ey*), and are directed backwards along the sides of the body, their apical portions curling round and lying alongside the first two pairs of legs. The joints of the antennae are ill-defined and hence their number cannot be made out with accuracy, but the difference in length of the antennae in the sexes is as marked as in the case of the adult insect. In the pupa of the male, the antenna usually curls forward to the base of the femur of the first pair of legs; in the case of the female the antennae curl forward to the apices of the tibia (*d*) of the first pair of legs and lie alongside the tarsi (*t*) (Fig. 13).

Attached to the prothoracic segment (*pr*) is the first pair of legs, which are folded underneath the body (Fig. 11), and show the typical parts, coxa (*n*), femur (*f*), tibia (*d*), the tarsus (*t*).

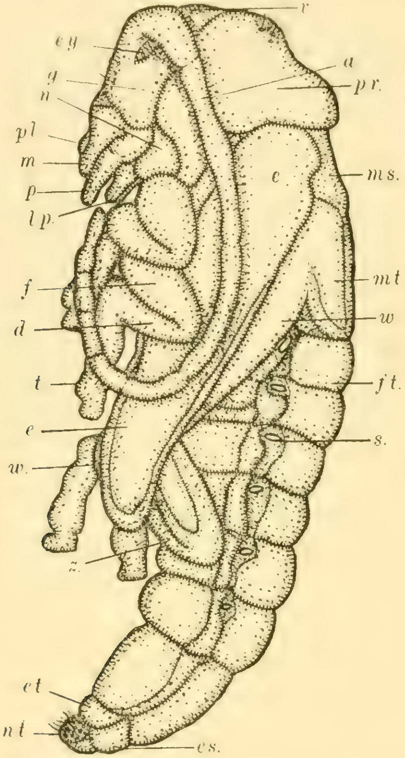


Fig. 11. Pupa of *S. carcharias*, female, side view (greatly magnified). *a* = antenna; *d* = tibia of leg; *e* = elytra; *es* = eighth tergite; *et* = eighth sternite; *ey* = eye; *f* = femur of leg; *ft* = first tergite; *g* = gena; *lp* = labial palps; *m* = mandible; *ms* = mesonotum; *mt* = metanotum; *n* = coxa; *nt* = ninth sternite; *p* = maxillary palps; *pl* = labrum; *pr* = pronotum; *s* = spiracle; *t* = tarsus; *v* = vertex of head; *w* = wing; *z* = hind leg.

The mesothoracic segment (*ms*) bears the elytra (*e*) or wing-covers. These lie between the body and the first two pairs of legs, and extend in a postero-lateral direction, their tips lying directly underneath the body. The mesothoracic segment also bears the second pair of legs. The metathoracic segment (*mt*) has attached to it the wings (*w*), which are flattened against the under surface of the elytra (e). Each wing projects in part beyond the outer margin of the elytron, under which it lies. The metathoracic segment also bears the third pair of legs (z) which lie between the body and the elytra.

The mesothoracic segment and the first five abdominal segments carry each a pair of spiracles (s). The spiracles are oval in shape. The thoracic spiracle, as in the larva, is far the largest one.

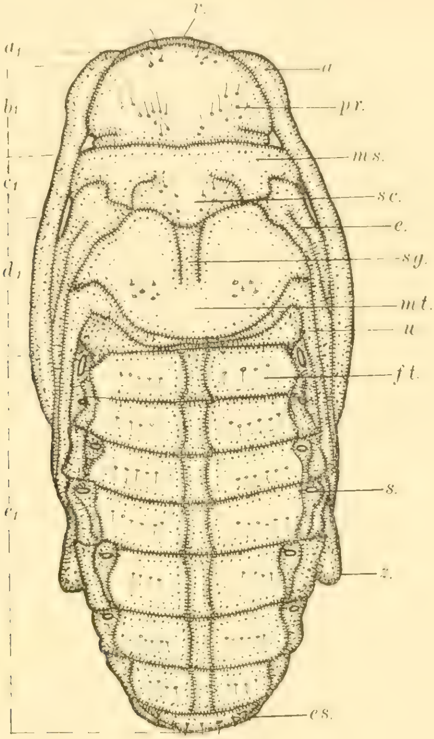


Fig. 12. Pupa of *S. carcharias*, dorsal view (greatly magnified). a_1 = head; b_1 = first thoracic segment; c_1 = second thoracic segment; d_1 = third thoracic segment; e_1 = abdomen; sc = scutellum; sg = scutellar groove; other letters as in Fig. 11.

In the dorsal view of the pupa (Fig. 12) it is seen that all the segments of the thorax and abdomen bear bristles, the prothoracic (pr) bristles being more marked than those of the other segments.

In the centre of the mesothoracic segment (ms) lies the scutellum (sc), while the metathoracic (mt) shows a fairly wide longitudinal groove, the scutellar groove (sg).

In the ventral view of the pupa (Fig. 13) the various parts of the head and mouth are clearly discernible. Anteriorly lies the vertex (*v*) and in the centre the frons (*fr*); on each side is the gena (*g*) or cheek region. The mandibles (*m*) are attached to the frons; between them lies the triangular labrum (*pl*). Below the mandibles are the labial palps (*lp*) in the centre, and on each side, a maxillary palp (*p*).

The ventral surface of all the abdominal segments with the exception of the last two is smooth. The penultimate or ninth abdominal segment (*nt*) bears on its lateral margins a patch of stiff bristles. The last or anal segment is somewhat triangular in shape; it is enclosed by the eighth (*et*) and the ninth (*nt*). There is a strongly marked sexual difference between the anal segment of the male pupa and that of the female (see Fig. 14). In the male (Fig. 14 *b*) this segment shows the anal opening (*an*) with a small membranous plate (*c*) trapezoidal in shape on its anterior margin;

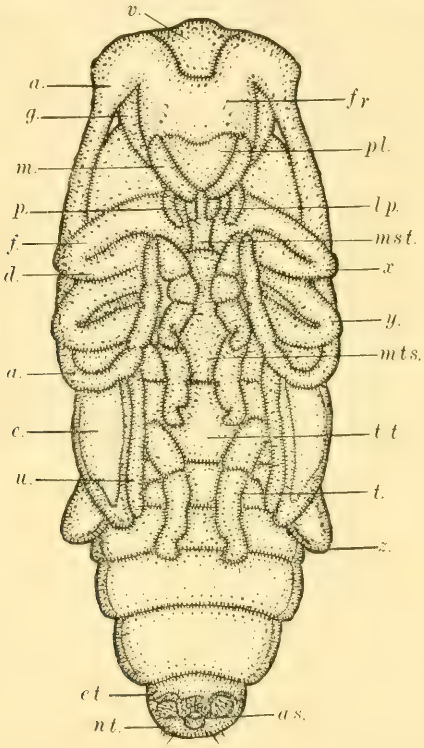
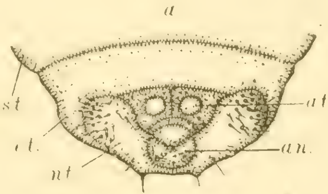


Fig. 13. Pupa of *S. carcharias*, ventral view (greatly magnified). *as* = anal or tenth segment; *fr* = frons; *mst* = mesosternum; *mts* = metasternum; *tt* = third sternite; *x* = first leg; *y* = second leg; other letters as in Fig. 11.

in the female (Fig. 14 *a*) instead of the membranous plate there are two globular tubercles (*at*) placed anteriorly side by side.

THE REPRODUCTIVE ORGANS.

Saperda carcharias has, in my observation and breeding of it, a short adult life in comparison with some Curculionid and Scolytid beetles, only about two months, and its reproductive organs, though not quite mature on the issue of the imagines from the pupal condition, ripen in a short time.



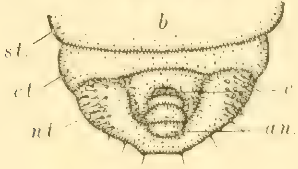


Fig. 14 *a*. Ventral view of the last three abdominal segments of female pupa of *S. carcharias* (greatly magnified). *an* = anus; *at* = anal tubercle on tenth segment; *et* = eighth sternite; *nt* = ninth sternite; *st* = seventh sternite.

Fig. 14 *b*. Ventral view of the last three abdominal segments of male pupa of *S. carcharias* (greatly magnified). *c* = membranous plate; other letters as in Fig. 14 *a*.

The male reproductive organs of Saperda carcharias.

The reproductive organs as dissected out from a male are shown in Fig. 15. They are made up of the usual parts, testes (*ts*), vasa deferentia (*vd*), seminal vesicles (*sv*), common or ejaculatory duct (*cd*), internal sac (*is*)[1] and the chitinous pieces, viz. median lobe (*ml*), tegmen (*t*), and spiculum gastrale (*sp*).

The testes (*ts*) are paired glandular bodies and lie on each side of the abdomen ventrally. Each body is dull yellow in colour and one lies more anteriorly in the abdomen than the other. Viewed laterally, each body is flattened from above downwards, and is rounded at the edges. In both ventral and dorsal view each appears as a round-shaped disc with a cavity in the centre. From the centre of the cavity on the ventral surface of the more anterior body, a tube arises which passes into the other body of the same testis, entering it at a point on the second corresponding to that from which it takes origin.

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[1] In this description I have followed the terminology adopted by Sharp and Muir in their studies of the male genitalia in Coleoptera. In these studies the nomenclature of the earlier workers is reviewed and criticised *Trans. Entom. Soc. Lond.* 1912, Part III, pp. 477 *et seq.* "The comparative anatomy of the male genital tube in Coleoptera," Sharp and Muir. Also same *Journal*, 1918, Parts I and II, pp. 209–229. "Studies in Rhyncophora," D. Sharp, and "Notes on the Ontogeny and Morphology of the male genital tube in Coleoptera," F. Muir.

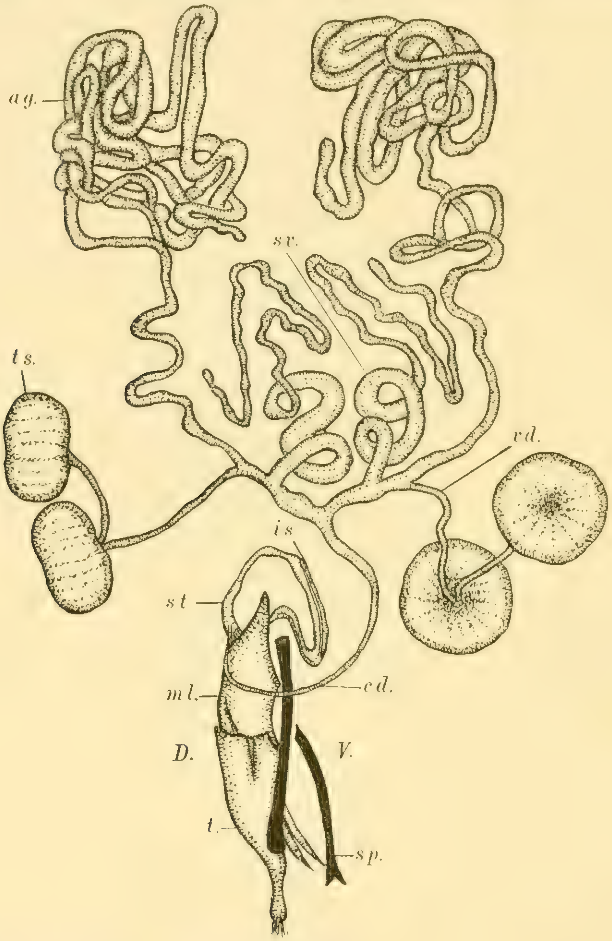


Fig. 15. Male reproductive organs of *S. carcharias* (greatly magnified). The chitinous parts are here shown in side view. *ag*=accessory gland; *cd*=common or ejaculatory duct; *D*=dorsal side of median lobe; *is*=internal sac; *ml*=median lobe; *sp*=spiculum gastrale; *st*=tube ensheathing the common duct; *sv*=seminal vesicle; *t*=tegmen; *ts*=testes; *V*=ventral side of median lobe; *vd*=vas deferens.

Just where this tube which forms the attachment between the two halves of the testis enters the more posterior body, another longer tube arises from the cavity. This tube is the vas deferens (*vd*). Each vas deferens is at first a narrow tube, which later swells out and ultimately unites with the vas deferens of the other testis, to form the common or ejaculatory duct (*cd*), leading to the internal sac (*is*) and the median lobe (*ml*).

This attachment of the glandular bodies of the testes is most interesting, as it would seem to indicate that the sperms produced in the more anterior body would have to pass through a part of the other body at least, before entering the vas deferens.

At the point where each vas deferens begins to swell out, the duct of the accessory gland (*ag*) opens into it. This gland, at its beginning, is much convoluted and ends blindly. A little further along each vas deferens, another tube, the seminal vesicle (*sv*) opens into it. This tube at its beginning is narrow; but for about a third of its length, prior to entering the vas deferens, it is much swollen and usually coils twice.

The common or ejaculatory duct (*cd*), at first a fairly wide tube, becomes more delicate and at last becomes hidden to view, ensheathed in a wide membranous tube (*st*) which is attached by muscles to the dorsal anterior surface of the median lobe (*ml*). In its course the common duct (*cd*) passes from the ventral side of the abdomen to the dorsal, and after passing through the ensheathing membranous tube (*st*), empties itself into the internal sac (*is*).

Passing into the membranous tube along with the common duct are two bundles of tracheae, which, later, enter the internal sac over the surface of which they ramify.

The internal sac into which the common duct empties itself is at first a much swollen tube, but latterly it thins out and enters the chitinous median lobe (*ml*) through the median foramen (Fig. 18 *a*, *mf*), terminating at the median orifice (*mo*) (see Figs. 16 *a* and 18 *d*).

The membranous tube (*st*) ensheathing the ejaculatory or common duct, and the internal sac, do not lead straight to the median orifice but bend several times in their course. The course of the internal sac with its various bends can be followed in Fig. 16 *a*.

At several points on the inner (external when exserted in the act of copulation) walls of the internal sac there are present chitinous structures which form the armature (see Fig. 16). On the swollen portion of the internal sac, *i.e.* between the termination of the membranous tube ensheathing the common duct and the first bend on the sac, there are present on its ventral wall three chitinous rods (*r*). Each rod is somewhat broadened at the end of the sac next the membranous tube and is pointed at the other end.

On the ventral surface of that portion of the sac between the first and second bend, there is placed a sheet of thin chitin (*cp*), which, under the high power of the microscope, shows a radula-like surface (see Fig. 16 *b*).

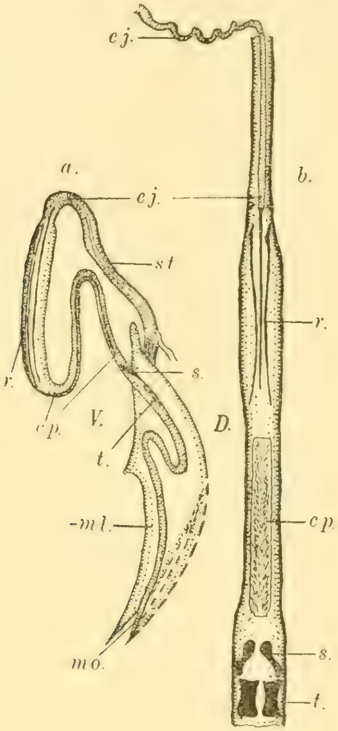


Fig. 16 *a*. Side view of internal sac and the median lobe; the latter is cut open to show course of the former; the tegmen is here removed (highly magnified).

Fig. 16 *b*. Portion of the internal sac bearing the armature is shown here straightened out (highly magnified).

cp = chitinous plate; *D* = dorsal side of median lobe; *ej* = common or ejaculatory duct; *ml* = median lobe; *mo* = median orifice; *r* = rods; *s* = first pair of chitinous rods; *st* = membranous tube; *t* = second pair of chitinous rods; *V* = ventral side of median lobe.

Just as the internal sac enters the median lobe there are present two pairs of short, stout chitinous rods.

The first pair (*s*) is placed on the lateral surfaces of the sac and arch over from the dorsal to the ventral surfaces (see Fig. 16, *s*).

The second pair of rods (*t*) lie adjacent to each other on the dorsal surface of the sac and are stouter than the first pair.

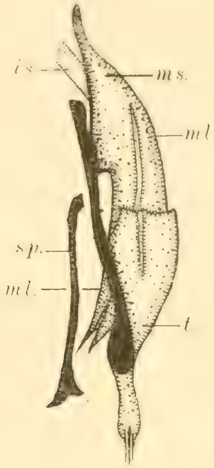


Fig. 17. The median lobe, tegmen, and spiculum gastrale, seen in side view, in their natural position (highly magnified). *is* = internal sac; *ml* = median lobe; *ms* = median strut; *sp* = spiculum gastrale; *t* = tegmen.

The median lobe (*ml*), roughly speaking, consists of a hollow curved cone of chitin pointed at its apical end. At the basal end, its dorsal surface is split into two parts called the median struts (*ms*) (Fig. 18 *a*).

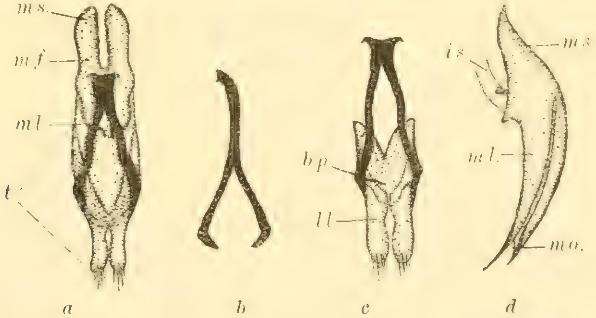


Fig. 18. The median lobe, spiculum gastrale, and tegmen showing their various parts (highly magnified).

Fig. 18 *a*. Ventral view of the median lobe within the tegmen.

Fig. 18 *b*. Ventral view of spiculum gastrale.

Fig. 18 *c*. Ventral view of tegmen.

Fig. 18 *d*. Median lobe, side view; tegmen removed.

bp = basal piece; *is* = internal sac; *ll* = lateral lobes; *mf* = median foramen; *ml* = median lobe; *mo* = median orifice; *ms* = median strut; *t* = tegmen.

For about three-quarters of its length, measured from the apical end, the median lobe is split into a dorsal and ventral portion by a membrane running along each of its sides from the median orifice (*mo*) (Fig. 18 *d*).

Ensheathing the median lobe at its pointed end is a circular ring of chitin called the tegmen (*t*). This tegmen shows a basal piece (*bp*) (Fig. 18 *c*) to which are attached two lateral lobes (*ll*). These last named portions bear on their apical parts a few stiff bristles.

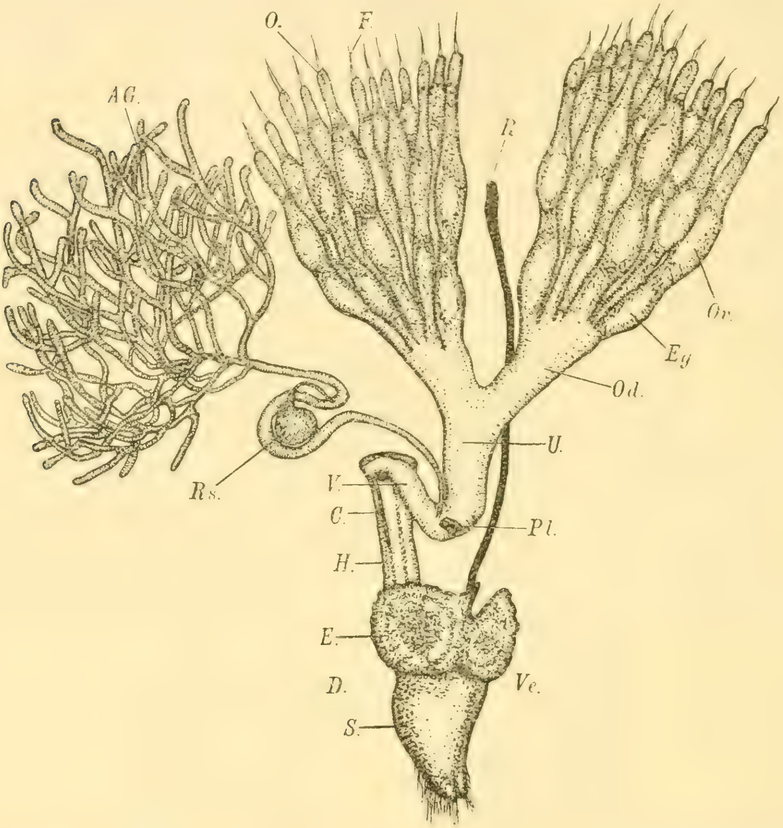


Fig. 19. Reproductive organs of female, *S. carcharias*, about to lay eggs (greatly magnified). The chitinous portions are shown in side view. *AG*=accessory gland; *C*=support in membranous tube of ovipositor; *D*=dorsal side of ovipositor; *E*=ear of ovipositor; *Eg*=egg; *F*=terminal filament; *H*=membranous tube of ovipositor; *O*=terminal chamber of egg tube; *Od*=oviduct; *Ov*=egg tube; *Pl*=chitinous plate on uterus; *R*=stout chitinous rod of ovipositor; *Rs*=receptaculum seminis; *S*=sheath of ovipositor; *U*=uterus; *V*=vagina; *Ve*=ventral side of the ovipositor.

Ventrally, the tegmen supports a stout chitinous arch.

The spiculum gastrale is an inverted Y-shaped piece of chitin and lies on the ventral side of the median lobe. The anterior arm of the spiculum gastrale is bent towards the dorsal surface, while the two posterior arms are somewhat hooked.

For purposes of comparison the various names of the chitinous parts of the male reproductive organs, used by Sharp and other authors, are brought together in the following table.

Lindemann (5)	Verhoeff (6)	Hopkins (7)	Nusslin (8)	Sharp and Muir (9)
Stengel	Spiculum gastrale	Fork	Spiculum gastrale	Spiculum gastrale
Gabel	Gabel	Ring	Gabel	Tegmen
Korper	Penis	Stem	Penis	Median lobe
Füsschen	Femora	Femora	Füsschen	Median struts

The Female Reproductive Organs of Saperda carcharias.

Fig. 19 shows the parts of the female reproductive organs dissected out of a beetle ready to lay her eggs.

There are two ovaries (*Ov*), one on each side of the abdomen. Each ovary consists of twelve egg tubes, each of which has a terminal chamber (*O*) with a filament (*F*) at its apex.

The eggs (*Eg*) pass from the ovaries to the oviducts (*Od*) which unite to form a common tube the uterus (*U*). Entering the posterior portion of the uterus dorsally, we have the accessory gland (*AG*) and the receptaculum seminis (*Rs*) (spermatheca).

The accessory gland, at its beginning, is composed of a series of branched tubes each of which ends blindly. Later these branches unite to form a single tube which at first is somewhat delicate.

Further along its course, the duct of the accessory gland swells out a little, finally thinning out again into a more delicate tube before it enters the uterus.

Just before the duct of the accessory gland swells out, the receptaculum seminis opens into it. The receptaculum seminis is a globular or bulb-shaped, chitinous body and lies in a bend of the duct of the accessory gland.

On each side of the uterus at its basal end is situated a chitinous plate (*Pl*). This plate, under the high power of the microscope (see Fig. 20, 1), shows a ridge (*ri*) running in a horizontal direction, dividing the plate into two halves.

Following the uterus (*U*) is the vagina (*V*), which bends forward towards the ovipositor, into which it passes.

Entering into the tubular portion of the ovipositor (see below) along with the vagina, are two bundles of tracheae ventrally, and the alimentary canal dorsally.

The ovipositor is made up of several parts—a membranous tube (*H*), a chitinous hollow sheath (*S*) and a stout chitinous rod (*R*). The membranous tube (*H*) bears several ridges on its inner surface, and enters the chitinous sheath (*S*) at a point about half way down the dorsal surface of the latter. The anterior end of the membranous tube is supported by a shears-shaped structure (*C*). This structure is made up of two chitinous plates (the handles of the shears) separated by a thin strip of membrane (see Fig. 20, *C*), and two membranous parts (the blades of the shears) darker coloured at their points on which are situated a few bristles.

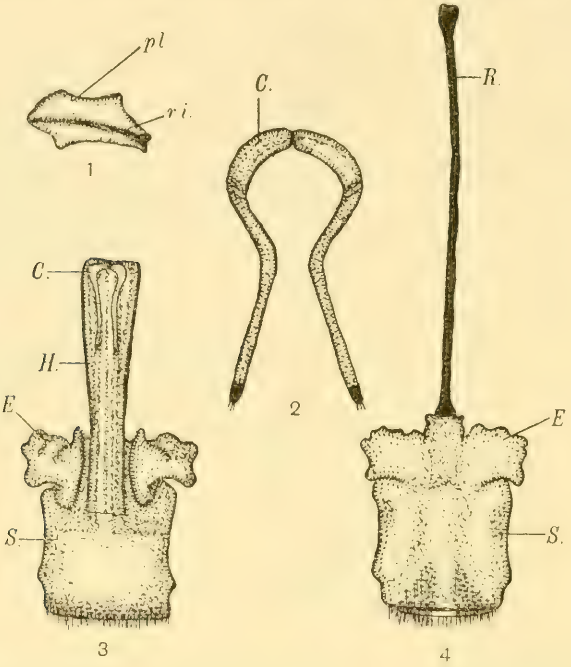


Fig. 20. Chitinous plate on uterus and the parts of the ovipositor (greatly magnified).
Fig. 20 (1). Chitinous plate at base of uterus.
Fig. 20 (2). Support in membranous tube of the ovipositor.
Fig. 20 (3). Dorsal view of membranous tube and sheath (rod portion of ovipositor removed).
Fig. 20 (4). Ventral view of ovipositor.
C = support; *E* = ear of sheath; *H* = membranous tube; *pl* = plate on uterus; *R* = rod of ovipositor; *ri* = ridge on plate of uterus; *S* = sheath of ovipositor.

The chitinous parts of the support lie on the inner dorsal surface of the membranous tube, while the membranous parts curve over to the ventral surface fitting into the chitinous ridges there.

The sheath portion (*S*) of the ovipositor bears on each side anteriorly an ear or wing (*E*); each wing has both a dorsal and a ventral projection. The membranous tube (*H*), already referred to, passes between the dorsal projections of the wings. These wings or ears afford suitable surfaces for the attachment of muscles, some of which play a part in the working of the ovipositor.

Borne by the anterior part of the sheath ventrally and projecting into the abdomen almost as far as the metathorax, is a stout, chitinous rod (*R*). This rod is about two and a half times the length of the sheath itself and shows grooves and ridges on its lateral surfaces. The posterior portion of the sheath is flattened dorso-ventrally and bears numerous bristles on its apical parts.

How the ovipositor is pushed out and withdrawn again I am unable to state, but three pairs of muscles which no doubt play a part in its working are worthy of note. The first pair stretches from the tip of the rod (*R*) to the anterior half of the chitinous plate (*pl*) on the uterus (*U*) (see Fig. 19). A second pair passes from the posterior half of the chitinous plate (*pl*) and attach themselves to the inner ventral surface of the sheath, while a third pair runs between the posterior half of the chitinous plate on the uterus and the ventral side of the membranous tube (*H*).

THE HABITS OF THE ADULTS.

Feeding. As soon as the adult insects issue from the stems in which they have developed, they crawl up to the leaves and proceed to feed on them.

During the daytime they do not feed to any great extent but remain motionless on the leaves; feeding takes place mostly in the evenings.

The males, after they have fed for some time, become more restless than the females and fly about from one clump of trees to another; often the males would take a bite out of a leaf here and another there, and then fly away to another tree. As far as I observed both sexes prefer the leaves of trees from three to twenty years of age.

The damage done by the beetles to the leaves is characteristic, and, in the absence of the beetles themselves, can be used as evidence that the beetles are or have been in the neighbourhood. The beetles always commence to feed on the surface of the leaf, never at the margin. Once a hole is cut through the leaf, the adult bites round and round the cut, gradually enlarging the hole. The result is that the whole of the centre of the leaf may be completely eaten out, and only the marginal portion left intact (Fig. 21). The holes so made are of various patterns; they may be circular, oval, elongate, or irregular, but in every case the serration caused by the large biting mandibles of the adults, is distinct. By way of contrast Fig. 21 shows two different kinds of damage. In this figure the leaf on the left shows the work of an adult of *S. carcharias* in its centre, while on its edge, at the right side of the base of its stalk, is the work of a Lepidopterous larva.

Flight. Both sexes have ample powers of flight but the males being lighter than the females fly with greater ease and much more frequently. Taken indoors, both sexes fly readily, but in the open the females are very restful.

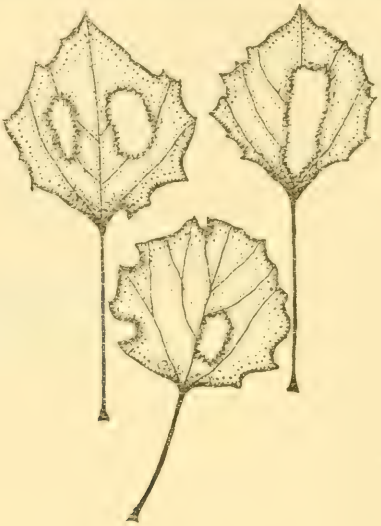


Fig. 21. Leaves of *Populus tremula* Linn. (natural size), showing characteristic injury by *S. carcharias* adult.

In the open the male beetle can soar to a considerable height. On several occasions I have noticed them as high as 30 ft. in the air. They can also fly a considerable distance at one time. The beetle in flight recalls a biplane. The outstretched elytra, held almost at right angles to the body, represent the upper plane, while the membranous wings stretched almost parallel to the elytra, correspond to the lower plane. A loud humming sound accompanies the flight of the beetle.

Stridulation. If live specimens of either sex of *Saperda carcharias* are disturbed or touched by the hand, they emit a fairly loud uniform chirping noise which varies in intensity. This sound is produced through the rubbing of the hind margin of the pronotum upon the central anterior portion of the prolonged mesonotum. These two portions form the stridulating organs and both of their surfaces are smooth and highly polished. On the insect moving its head slowly up and down, friction is caused by the rubbing of these two polished areas upon each other, and as a result a noise is produced. The same sound can be produced in a dead beetle by imitating this action.

Pairing. The mating of the sexes takes place on the twigs and smaller branches of the trees upon which they feed. On one occasion pairing was found on a leaf. As a rule pairing occurs during the daytime and the beetles may remain in copula over night; the length of the time two beetles may remain coupled is extremely variable.

The males seemed to outnumber the females. They certainly did in the areas examined, where I estimated the proportion as 5 to 1. In my opinion the males are attracted or guided to the females through sense of smell. On one occasion I observed a male soaring in the air about fifteen yards away make a direct flight towards a female, already attended by two males, and alight beside her.

Oviposition. The female deposits her eggs in the stems of vigorously growing, healthy trees, and near the base. Prior to egg-laying, a preliminary examination is made by the female of this portion of the stem. During this survey she rubs the apex of her abdomen on the bark of the stem, at the same time swaying her body from side to side. After testing in this manner for a short time she crawls round and round the stem often returning in the opposite way. Finally when satisfied, she chooses a spot on the surface of the stem where the bark is smooth, and standing with her body at right angles to the long axis of the stem, her antennae directed backwards along the sides of her body, she gnaws a notch with her mandibles. The incision lies typically in the vertical direction, but sometimes is tilted slightly (Fig. 22). The cut measures on an average about 4·75 mm. in length. The depth of the cut varies, but on an average is about 2·25 mm. On very young stems, where the bast layers are thin, the incision usually reaches the sapwood; on older stems, *e.g.* from twelve years old and upwards, where the bast is thicker, only the outer layers of the bast are cut.

The time taken for completing the egg cavity is about ten minutes or longer, and then the female turns round and backs into the excavation, locating it with the tip of her abdomen. Next taking a firm hold of the bark, resting mainly on her middle and hind pairs of legs, she thrusts out her ovipositor, inserts it into the incision and forces an egg through it. Before the ovipositor is withdrawn, a colourless gummy fluid is passed into the egg-incision. During this operation much muscular effort is expended, for the egg is pushed away from the egg-bite. Where the bast layer is thin, *e.g.* on stems between five and twelve years old, the egg is found firmly placed between the cambium layer and the sapwood. and about 2·5 mm. from the egg-bite. On the other hand, if the stem be older and the bast layers thicker, the egg is placed between the tissues of the bast.

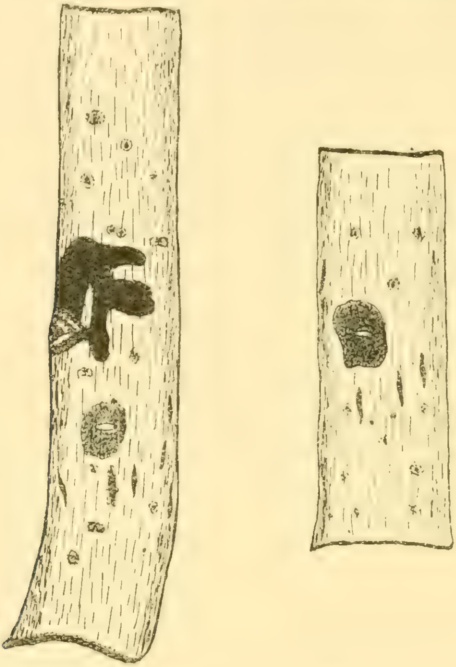


Fig. 22. Lower nine inches of 6–7 year old poplar stems showing egg-incisions and burrowings of young larvae (dark patches in figure). Two eggs and the young larval burrowings are here exposed by the tearing away of the bast and cambium layers.

The spot selected by the female for egg-laying is always a smooth portion of the stem. On no occasion have I found her laying eggs in cracks or lenticels. I am inclined to believe that the statement in continental works that eggs are laid in cracks, is due to the fact that the actual egg-laying of the beetles has not been observed, the eggs having only been noticed when the egg-incisions had begun to gape, viz. in about one month's time from the date of laying. These cracks have been suggested as places chosen for egg-laying, the real fact being that the crack is the result of the egg-laying.

One egg only is inserted into each incision. It is quite a common occurrence, however, to find on badly infested stems, two or more eggs placed close to one another, but careful examination shows that each egg has been forced into a separate incision.

On several occasions one found females inserting their ovipositors into egg-bites without eggs being laid. It is a common occurrence to find more egg-bites on stems than there are eggs.

Owing to the position taken up by the female during oviposition, namely, with her body at right angles to the long axis of the stem, the eggs are always placed with their long axis in the horizontal direction (Fig. 22); exceptionally eggs were found slightly tilted.

The time taken for the egg-laying process is variable. In one case I observed that a female remained in the egg-laying position for five and a half minutes, while on another occasion she remained thirty-two and a half minutes.

The egg-bites, when newly cut, and into which eggs have been inserted are very narrow, to the eye appearing as a thin line, and until one gets familiar with their appearance they are very apt to be overlooked. In course of time the bites open or gape, and ultimately show as longitudinal dark cracks. In this stage they are very readily detected on the surface of stems. These bites are the only external evidence of the presence of eggs.

The total number of eggs laid by a single female is variable. The lowest number I ever counted was twenty eight while the highest was fifty-one. All the eggs are not laid on one stem, but spread over several. As a rule the younger the stem chosen the fewer the eggs laid on it. As an illustration, I have counted as many as ten to twelve eggs on several twelve year old stems, while seven was the average number on the five year old ones.

As will have been noticed in the study of the structure of the reproductive organs of an egg-laying female, all the eggs present in the ovaries are not mature at one time, a fact further borne out in the breeding experiments described later. Usually one finds on the dissection of the ovaries of a ripe female that only twenty-four eggs are mature at one time. The time taken to complete egg-laying is variable. In my experiments it extended from fourteen days to three weeks. In one particular case of egg-laying kept under close observation, as many as eight eggs were laid in a single day, and the female, after she had laid these, resumed feeding, and then returned to the base of the stem to complete her egg-laying. Sometimes egg-laying females were noticed to cut vertical notches much resembling egg-incisions, and so nourish themselves.

COLOURATION IN THE SEXES.

From a careful examination of a very large number of specimens of *Saperda carcharias* in the Aboyne areas, I have come to the conclusion that there are two colour varieties in the male. The majority of the males are covered with an ashy or white-grey pubescence, but others show a pubescence of a colour similar to the female, namely, greenish-yellow.

While the variety with ash-grey pubescence is the predominating variety in the Aboyne district, in other areas this variety is not nearly so plentiful.

In the Waterhouse Collection in the Entomological Department of the University of Edinburgh, none of the male specimens of *S. carcharias* show this ash-grey or white-grey pubescence.

Through the courtesy of Dr Gahan an examination was made of the collection of *S. carcharias* in the British Museum (Natural History Museum, South Kensington), but in only one example in the British collection was there any approach to the ash-grey variety, all the other specimens showed the greenish-yellow pubescence. Among the *S. carcharias* specimens from Central Europe, however, there were several males with ash-grey pubescence.

Professor Hudson Beare informs me that E. Reitter in his *Fauna Germanica*, vol. XIV. p. 64 refers to this ash-grey pubescence (ab. grisescens, Mulsant). Reitter states that specimens of this colour occur but rarely in Germany. Evidently the describer, Mulsant, makes no reference to or had not noticed this colour to be peculiar to the males. Professor Hudson Beare, in collecting specimens of *S. carcharias*, in England, has not yet met with males showing this ashy-grey pubescence.

On account of their colouration, while feeding on the leaves of their host plants, the males showing the greenish-yellow pubescence similar to the females, and the females themselves are rendered very inconspicuous (Plate XX, Right). Even while at rest on the twigs during pairing their mottled greenish-yellow colouring is to some extent effective as a means of concealing them.

In the case of the males of the ash-grey variety their concealing colouration is not conspicuous while feeding on the leaves of their host trees, but their colour accords exceedingly well with the ash-grey bark of the twigs and branches (Plate XX. Left). During oviposition the female is not a conspicuous object, as the basal portions of the stems chosen for egg-laying are in many cases either covered with moss, the colour of which blends well with the colour of the female, or she is entirely obscured to view by ground vegetation surrounding the stems. So effective is concealing colouration in this species, that until the eye gets accustomed by search, it is very easy to pass the beetles over; on one occasion an insect which was passed unnoticed, revealed itself by the stridulation which followed a jarring of the twig, on the leaves of which the insect was resting.

THE LARVAL GALLERIES.

Of the numerous completed larval galleries examined by me on stems not badly infested and where the larvae had room to work, one form of gallery was met with far more frequently than any of the others. This form may be taken as the typical gallery (see Fig. 23).

For the sake of description the typical form of gallery may be divided into four different portions, viz. (*a*) the initial or horizontal portion, (*b*) the vertical portion, (*c*) the exit portion, and (*d*) the pupal portion.

(*a*) *The initial or horizontal portion.*

Upon issuing from the egg, the larva feeds at first upon the egg shell and then proceeds to destroy the tissue immediately surrounding it, viz. the inner bast layers and the cambium. In this way a minute shallow roundish patch is formed. Later the larva works its way out of the egg cavity or patch and cuts into the sapwood in a horizontal direction. As it bores, some of the gnawed material is passed through its alimentary canal, but far more is passed backwards into the gallery. As a rule the sides of this horizontal portion of the gallery are very irregular in outline and are deeply indented. The shape too of this portion is constantly being altered, as the young larva returns along it, repeatedly widening and deepening it, at the same time clearing away the frass or gnawed material, so as to keep a free air-passage to the exterior through the now gaping egg-bite.

There is great variation in the length of this portion of the larval gallery. In some cases it was fully one inch in length, while in others it was only about half that length.

(*b*) *The vertical portion.*

When the initial portion is completed the larva turns downwards, that is to say, at right angles to the first portion. As the larva tunnels downwards, it gnaws gradually deeper and deeper into the sapwood until finally the centre of the stem is reached. On the root portion of the tree being reached the larva turns about and tunnels up the centre of the stem. This part, at the turning point, is much widened and is irregular in outline.

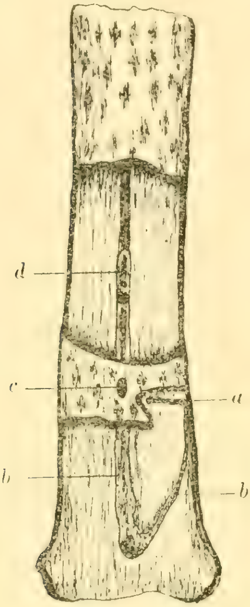


Fig. 23.

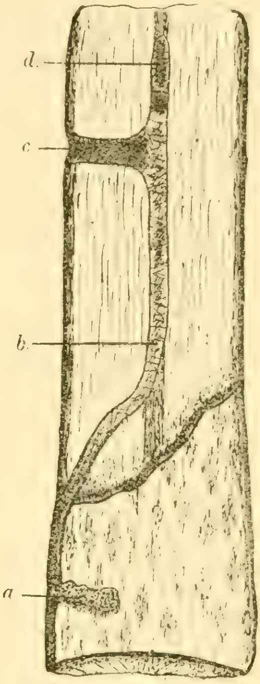


Fig. 24.

Fig. 23. Typical form of larval gallery on a 7 year old poplar stem. (The horizontal scale to which figure is drawn is much greater than the vertical.) *a*=horizontal or initial portion of gallery on outer layers of sapwood; *b*=vertical portion of gallery in wood; *c*=exit hole; *d*=pupal portion.

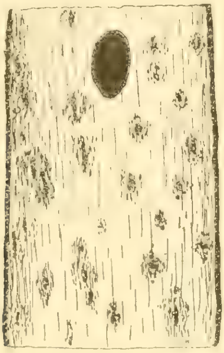
Fig. 24. Another form of larval gallery. Larva here after having tunnelled for some distance downwards proceeded and tunnelled upwards. *a*=horizontal portion of gallery on outer layer of sapwood; *b*=portion of gallery in wood; *c*=exit portion of gallery; *d*=pupal chamber.

(*c*) *The radial or exit portion.*

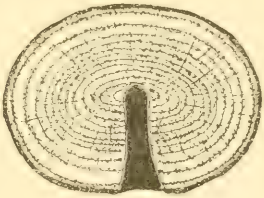
On its way up the centre of the stem the larva turns round and bores in the transverse direction, cutting through the sapwood and bast, and ultimately reaching the outside of the stem (see also Fig. 25). This portion of the gallery is regular in outline and is elliptical in section, its greatest breadth being in the vertical direction. In some cases, however, the exit hole appears only as a longitudinal crack on the surface of the bark. Usually the exit hole occurs about four to six inches above the level of the ground but in a few cases it was cut well up the stem, occurring as high as one and a half feet. As a rule this portion of the gallery is not completed all at once, but the larva returns again and again from the centre of the stem until it is completed. On the completion of this portion of the gallery the larva plugs it tightly with gnawed material.

(*d*) *The pupal portion.*

The larva now continues to bore up the centre of the stem in the vertical direction and may reach a height of 1 ft. 9 in. or 2 ft. in the centre of the stem. By this time it is full grown and is ready for pupation. Enlarging slightly the diameter of the portion of the tunnel just cut, *i.e.* the uppermost portion, it seals the burrow tightly behind it with a dense plug of coarse frass ripped roughly from the side of the gallery. This operation being completed, the larva now within its pupal bed, ceases to feed, reverses its position, its head-end resting on the plug of frass at the lower end of the cell, shrinks slightly, moults, and the pupa is revealed. The moulted chitinous head parts of the larva are found lying in the upper end of the pupal chamber. The length of the pupal chamber is on an average 1½ inches.



a



b

Fig. 25 *a*. Portion of stem of a 12 year old poplar showing oval exit hole made by larva for exit of adult.

Fig. 25 *b*. The same in transverse section to show the complete exit portion of gallery.

The time taken by the larva for the completion of the whole gallery, excluding the hibernating period, is about eight and a half months.

After the period of pupation has passed, the young imago bores through the plug of frass at the base of the pupal chamber, and then gradually works its way down the centre of the stem to the exit portion of the gallery. Clearing away the frass of the exit portion, and at the same time widening and rounding off its outline, the adult finally reaches the outside and issues through the now circular exit or flight hole.

If such a gallery as that described be made on a very young stem, say a stem about five years old. one finds that the whole of the wood in the centre of that portion of the stem between the exit portion and the pupal chamber has been cut out, and only a thin outer shell remains.

Another form of gallery is that shown in Fig. 24; a modification of the form just described; it may be found in older stems. Here the larva, after tunnelling the horizontal portion of the gallery, turns at first downwards for a short distance and then returns and tunnels upwards, gnawing deeper and deeper into the sapwood, until the centre of the stem is reached. Before pupating, the larva cuts the exit portion at the upper end of the gallery, pupating as in the case of the typical form.

Irregular Larval Galleries (Plates XXI and XXII).

Where many larvae are at work together on a stem, their galleries may be very irregular both in shape and in direction. In fact, in many cases it is extremely difficult, and may be impossible, to trace an individual gallery at all. As some of the less irregular forms are merely modifications of the typical gallery, I propose to describe the parts of them in so far as they differ from the forms already described.

A specially common case is where the centre of the stem has already been tunnelled by an older larva. Here, the younger larva cuts the vertical portion of the gallery in the wood alongside the gallery already cut in the centre of the stem. In other respects the gallery cut vertically upwards by the younger larva resembles that of the typical form of gallery, only it is much shorter. Whereas the typical form of gallery cut in the pith may reach a length of almost 2 ft., it may only reach 9 inches in the irregular form. The outline too of the gallery when cut in the wood is different from that when cut in the pith. In the case of the former it is oval, elliptical or irregular in section, whereas in the latter it is almost circular.

In other cases occurring under similar circumstances to the last, but where old flight holes are already present on the stems, and within easy reach of the younger larvae, no exit hole is cut, the future imagines issuing through old flight holes. On young stems of about five years of age it was a common occurrence to find the horizontal portions of the larval galleries running into each other, with the result that the stems were completely ringed. After the larvae had completed this portion of their galleries, they would turn downwards in the stem, completing their tunnels in one of the ways already described.

As a general rule, on very badly infested stems and where these had already been badly holed by larval tunnels, the younger larvae would tunnel in any direction where the wood was intact and make no provision for the exit of the imagines, leaving these to escape through old flight holes.

In exceptional cases, on badly tunnelled stems, the adults cut their own flight holes, choosing a part of the stem where the outer bark was fissured or where it was thin.

The Habits of the Larva in the Stem.

The manner in which the larva propels itself in the stem during feeding and the cutting of the gallery is very interesting, as apparently it can ascend or descend with equal facility. The grubs are legless, but locomotion is secured through the use of well developed dorsal and ventral ambulatory ampullae, which come into play either from the anterior or posterior end of the body in peristaltic succession. These ampullae, together with the chitinous asperities on the dorsal surface of the prothorax, braced against the sides of the gallery, constitute an efficient and rapid means of locomotion. In descending the stem the various movements may be reversed, but most commonly the larva descends head in front.

During the gnawing process the head and thorax are moved with a sidewise motion, and in this way the wood is bitten off. Some of this gnawed material is passed through the alimentary canal, but by far the most of the material is passed behind into the gallery, and is either pushed to the outside of the stem through an egg-incision or exit hole, or is pressed tightly to the sides of parts of the gallery.

The young larvae when present in large numbers in a stem develop a cannibalistic habit, and often one finds on tracing the galleries in such stems, that some of them end very abruptly. If, experimentally, a few larvae of different sizes be placed together in a box for a short time, say for an hour, the smaller ones on being examined at the end of this period will be found to have been badly bitten by the larger ones, and they subsequently die.

THE LENGTH OF THE LIFE CYCLE.

My first observations on *S. carcharias* in the open, began in Aberdeenshire, in 1915, but it was not till the following year that any definite experiments were begun with a view to the determination of the length of the life cycle.

On July 10th, 1916, in the areas where the poplars were infested with this species, I noticed on examination of a number of stems of various ages that quite a large number of young larvae were present underneath the outer bark layers. These larvae had not been long hatched, for they had just cut the tissue close to where the eggs had been deposited and had just begun to cut the horizontal portion of their galleries. To facilitate observation of these larvae later on, small notches were cut. Throughout the summer and autumn these marked stems were examined with a view to following the making of the larval burrows. Till September 28th, 1916, the larvae continued to burrow in the stems, but about this time they ceased feeding. In all the cases examined at this time the larvae had completed the horizontal portion of their galleries, and had also tunnelled the portion of their gallery in the vertical direction downwards, reaching almost the roots of the trees. In all cases the larvae hibernated head downwards. Their average length at this stage was 18 mm.

In the end of March, 1917, six of these marked plants were carefully removed from their natural habitat and replanted in an area where they could be kept under closer observation and at the same time be protected from further infestation. These young trees chosen for replanting were from five to seven years of age as at these ages they could be transplanted without undue risk to their life. Along with these marked stems four uninfested plants of a similar age were removed from the wood and replanted alongside the infested ones. Throughout the winter and early spring months, October, 1916, to March, 1917, the larvae hibernated. Examination of the stems on April 22nd, 1917, showed that the larvae were still hibernating. From April 25th, 1917, to May 5th, 1917, they showed signs of movement within their burrows, but did not recommence to tunnel and extend their galleries till about May 8th, 1917. Throughout the summer and autumn of 1917, the larvae continued to tunnel in their burrows. On October 2nd, 1917, they ceased to feed. At this date some of the larvae had attained their full growth and had completed their pupal chambers.

From October, 1917, to December, 1917, the stems containing the full-grown larvae were examined at intervals, but no signs of pupation were shown. From January, 1918, to April, 1918, they were not examined, as during this period I was engaged in Forest Survey work for the Board of Trade Timber Supply Department. On May 16th, 1918, I re-examined these stems but still there were no signs of pupation. On May 22nd, 1918, the first larva pupated; others continued to pupate up to June 4th, 1918.

The larval period then from July 10th, 1916, to May 22nd, 1918, was about 23 months. When emergence of the adults was near at hand, the stems were screened with slips made from draper's cotton so that the adults when they emerged from the stems would not escape into the open; the adults were secured. The adult stage was reached by one female on July 2nd, 1918, but she did not emerge through the exit hole till July 14th, 1918. That is to say, the pupal stage from May 22nd, 1918, to July 2nd, 1918, lasted about forty days. Many adults, the majority of them males, issued from the stems up to July 31st, 1918. As these adults came away from the stems and collected in the cotton slips they were caught and placed in fresh cotton cages. Each cage consisted simply of a slip of cotton drawn over each of the four uninfested transplanted stems already referred to. As the foliage of the trees could not be enclosed conveniently within the cotton cage, each slip at its upper end was tied closely round the stem, while the lower end of the slip next the ground was weighted down with stones and soil. In this way a complete cage was formed and the beetles could not escape. In each cage a wide-necked bottle of water was enclosed, containing young twigs bearing leaves of the Trembling Poplar (*Populus tremula* Linn.), so that the beetles could feed on the leaves if they chose. Fresh twigs were placed in the bottles in the cages every second day. Immediately the beetles were placed in the cages they made for the leaves on the twigs and greedily devoured them.

The first pair of beetles was placed in a cage on July 16th, 1918, and a constant watch was kept for pairing, but copulation did not take place till July 26th, 1918, the beetles having fed for eleven days. As soon as pairing was observed, the pairs were marked by simply breaking off the tip of an elytron, so that they could be readily recognised. Three days after having paired, the first male beetle died. Oviposition of the first female was noticed to take place at the base of the stem enclosed in the cage, on August 2nd, 1918, and egg-laying was completed by August 15th, 1918. As soon as egg-laying was completed the female no longer fed on the fresh leaves supplied, but clung to the sides of the cotton cage. This female lived until August 28th, 1918. In other cages similar observations were made, only the beetles lived somewhat longer. In some cases the females lived for three weeks after egg-laying was completed, while the males lived for one week after pairing.

During the period of egg-laying freshly cut pieces of stems of poplar were placed in all the cages so that plenty stem-surface would be given for the females to lay on. The eggs laid on the stems enclosed in the cages were examined at intervals to ascertain if any of them had hatched, but in no cases, even in those eggs laid as early as August 2nd, 1918, had larvae issued. Dissection of some of the eggs at the end of September, 1918, yielded young larvae.

Throughout the hibernating period, October, 1918, to May, 1919, the eggs on the stems were examined at intervals but always without any hatching. On examination of the stems on June 14th, 1919, however, some of the eggs present on the stems had hatched. Others hatched in the following days and by June 20th, 1919, all the eggs present on the stems under my notice had hatched. The egg stage in these experimental cases thus lasted about ten and a half months.

On the stems marked in July, 1916, left in the open under natural conditions, similar results were obtained as regards the length of both the larval and the pupal periods. Adults were found to escape from stems in the open—marked and unmarked—from July 16th onwards, and egg-laying was found to take place on the basal portions of the stems from August 4th, 1918, to August 25th, 1918. The principal period of emergence of the beetles was from mid July to mid August. During the period of oviposition in the open, a search of the infested areas was made for females that were laying eggs and also for fresh egg-bites. Where these were found, nicks were cut so that the places could be detected later. From August 4th, 1918, to August 25th, 1918, a large number of those egg-notches were marked. The marked stems were examined every three days throughout the late summer and autumn, but in only two cases were eggs found to have hatched. The date on which these were found was August 26th, so that the incubation period was in this case about three weeks. In all the other cases examined the eggs remained unhatched. Portions of these stems cut down in May, 1919, were kept in the open and examined at intervals, but not till June 15th, 1919, did any of the eggs on them hatch. The two cases where eggs hatched in late August, 1918, were exceptional and large numbers of stems containing eggs were examined.

During the summer of 1919 many egg-incisions were made by females between August 3rd, 1919, and August 12th, 1919, but up till now, December 11th, 1919, none of the eggs have hatched.

From experiments and from my observations made on eggs and larvae in their natural habitat, the length of the life cycle of *S. carcharias*, in Scotland, is about four years, a very considerable part of this time being passed in the over-wintering egg-stage. In warmer conditions than in Scotland, the period of the life cycle is shorter; for example, continental writers state that in Central Europe the typical length of the life cycle is three years.

As an illustration of the influence of temperature on the length of the life cycle, I may say, that from some pieces of stem cut down in the open on January 25th, 1919, containing fully-grown larvae ready to pupate, and kept under laboratory conditions, adults emerged during the first days of May, 1919, while in corresponding material left in the open, the larvae only reached the pupal stage on May 23rd, 1919, the adult stage on July 8th, 1919, and emergence followed on July 20th, 1919.

HOST TREES.

In the areas in Aberdeenshire, where my observations were made, *S. carcharias* is attacking one species of poplar, namely, *Populus tremula* Linn.

Adults, kept in the laboratory and offered the leaves of various species of poplar fed willingly on all of them. Further, in summer, 1919, females in captivity readily laid their eggs on pieces of stem of the Black Italian Poplar (*P. monilifera* Ait.).

In the following list, the poplar species attacked by *S. carcharias* are collated from the works of the continental authorities named below. Ratzeburg (10) records *S. carcharias* on Black Poplar; Altum (11) states that it attacks Canadian, Black and Trembling Poplars, and also willows; Schiodte (12) says that the larvae are found on *Populus monilifera*, *P. ontariensis*, *P. tremula* and on willows. Kaltenbach (13) names as host trees, *P. nigra*, *P. dilatata* and *P. tremula*; Tachenberg (14) names Black Poplar, Trembling Poplar, Italian and German Poplars, also willows. Judeich and Nitsche (15) state that the species is found on all poplars but most commonly on the aspen (*P. tremula* Linn.); Nusslin (16) confirms this statement and adds willows as host trees. A more recent record is a Spanish one, *S. carcharias* having been found on *P. nigra* in the province of Gerona (17).

ECONOMIC IMPORTANCE OF *S. CARCHARIAS*.

In the areas examined by myself, only vigorously growing healthy, trees between the ages of five and twenty years have been chosen for attack by *S. carcharias*; the species is therefore of considerable economic importance in our forestry. This importance lies not so much in the fact that the insect is attacking a species of poplar, namely, *Populus tremula* Linn., which is chiefly an ornamental one, but in the fact that in the absence of this host, or on a sudden increase of its numbers, as in the case of many other injurious insects, other valuable timber-producing poplar species would be endangered.

The destructive work of *S. carcharias*, both in the adult and larval stages, is partly of a physiological and partly technical nature. The adults, through their habit of eating out portions of the centre of the leaves reduce the leaf-surface of the tree, and in cases where the midribs of the leaves have been cut, the food supply is interrupted (see Fig. 21). Then there is a second kind of damage done by the adult, namely, the cutting of the egg-incisions on the basal portions of the stems (see Fig. 22). This is the more serious kind of adult damage, for, as a result of this gnawing of the egg-bites, the outer bark or bast layers and cambium may be cut. The insertion of eggs through these bites adds further to the injury of these layers. Later these incisions are the origin of the large deep fissures on the surface of infested stems. Further, the female beetles have the habit of cutting a large number of nicks on the basal portions of stems, of a similar appearance to egg-bites, but no eggs are inserted into them. Such incisions afford suitable openings or wounds for the entrance of spores of parasitic fungi. In any case should the cambium layer be destroyed in the cutting of these incisions, and this is very frequently the case in stems of small diameter, the injury gives rise to defects in the growth of the stem.

By far the greatest damage, however, is done by the larva. First of all, the larvae on hatching tunnel along the surface of the sapwood in a horizontal direction and as a result the inner bast layers, cambium and outer sapwood may be badly injured. Where there are several larvae at work, the stem can be completely girdled by the union of these horizontal tunnels and the flow of sap interrupted. On young stems, say, about five to seven years of age, the presence of only a few larval tunnels on a stem is sufficient to prevent the flow of sap. In several cases that came under my notice, the union of the horizontal portions of only two larval galleries completely ringed the stems.

Then there is the additional injury of a technical nature done by the larvae, namely, that caused through their tunnelling in the longitudinal direction in the wood of the stem (Plates XXI and XXII).

In cases where stems are badly infested with larvae, the whole of the wood may be completely riddled with such tunnels. As a result the commercial value of the wood is rendered worthless. These injuries to the wood by the larval burrowings do not alone directly cause the death of the tree. The death is due principally to injuries of the bast and cambium layers.

Further, the making of exit holes by the larvae in preparation for the issue of the imagoes, the widening of them by the imagoes, and consequently, the allowance of air and moisture into the centre of the stems, hasten still more the destruction of the wood. In many cases in which the stems had survived an earlier attack, the flight holes had been completely occluded through the growth of the outer bark layers and were completely hidden to view. Where all the wood is practically destroyed, or the stem sufficiently injured by the larval tunnels the tree is greatly weakened against wind. Hence it is not an uncommon occurrence on the examination of an infested area after a wind storm, to find many of the badly infested stems broken over at their bases.

In the areas under observation the damage done to the natural growth was very great, practically every tree from five to twenty-five years of age showed signs of infection in one stage or another. Some of the trees which had survived a bad infestation were still alive but showed a stunted growth, their bases being much swollen and bearing deep black fissures. Others had quite hollow stems, the wood in their centre having been completely destroyed (Plate XXIII).

It is evident then, that if artificial plantations or nurseries containing poplars were in the neighbourhood of areas where the natural growth was badly infested, the trees present in them would be greatly endangered and considerable loss would ensue from an attack.

EVIDENCES OF ATTACK.

The first indication that adults are present in any area of poplars may be known by examination of the leaves and stems of the trees. Should adults be present, holes on the leaves—the boundary of the wound showing serrations—will be found. This evidence of the presence of beetles is easily recognised once attention has been drawn to it, and I make special mention of this as at this stage the beetles could be looked for and collected before egg-laying had commenced or been completed.

As the principal emergence period of the beetles in Scotland, is from mid July to mid August, beetles should be looked for between these dates and collected.

To ascertain if the beetles have begun egg-laying, one has only to examine very carefully the surface of that portion of the stems between the level of the ground and nine inches upwards. As the reader will have noticed in an earlier paragraph, if egg-laying has begun, egg-bites will be found on these basal portions of the stems. These will have the appearance of short, thin, narrow markings, measuring about 4·75 mm. in length. To the left or right of each of these markings, lying either in the bast layers if these be thick, or between the cambium layer and the sapwood where the bast layers are thin, a single egg may be found.

At a later date, *i.e.* in about one month's time these bites develop into deep black cracks or scars, which, in course of time, become greatly lengthened.

As soon as larvae begin to groove the surface of the sapwood, their presence is indicated by the protrusion of coarse shreds of gnawed wood, which are thrust out through the egg-incisions. In the first year of larval life, the presence of larvae in infested stems is not well marked. It is while tunnelling the vertical portions of their galleries, that external symptoms of larval attack become very apparent. The presence of the larvae is then plainly indicated by large quantities of sawdust and wood chips, lying in heaps at the bases of the stems, having been pushed out by the larvae either through the exit hole or through cracks on the stem.

Then there is the presence of the exit holes which occur from the base to well up the stem. Should these holes be found on examination to be packed tightly with frass and to be oval in section, then the adults have not yet issued through them. On the other hand, if these holes be circular in shape and empty, then adults have escaped from the stem. In older stems which had survived earlier attacks, it was common to find the flight holes greatly enlarged, and appearing as longitudinal fissures on the surface of the stems (Plate XXIII).

Control Measures.

With a knowledge of the life history and habits of the species, it is now possible to make definite recommendations and suggestions for its control should it ever become necessary.

Trees grown both in natural regeneration and in artificial plantations, if already infested, should be cut down and burned, as they will be a source of danger to healthier trees. This operation should be carried out before the end of June of each year, so as to be completed before the beetles begin to emerge.

As soon as the presence of adults is indicated by the cutting of the leaves of the host plants, steps should at once be taken to seek out and collect as many of them as possible. These should be looked for, in Scotland, between mid July and the end of August.

If carried out, these two measures will ensure the destruction of a large percentage of the surviving larvae and beetles each year, so that the damage will be reduced to a minimum.

In the case of a few trees, *e.g.* park trees, oviposition may be largely prevented by ensheathing the lowermost portion of their stems, say, for a foot and a half above the level of the ground with netting of a close mesh, or by coating them with some deterrent substance or wash which would prevent the beetles from laying on them. A repellant wash, such as that mentioned in Mr R. N. Chrystal's paper (18) on the "Poplar Borer," *Saperda calcarata* Say, might prove useful. The formula is—

> In six gallons of saturated solution of washing-soda dissolve one gallon of soft-soap, add one pint of carbolic acid, mix thoroughly; slack enough lime in four gallons of water, so that when added a thick whitewash will result, then add one half-pound of Paris green; mix thoroughly.

NATURAL ENEMIES.

The larva of *S. carcharias* is parasitised by an Ichneumonid larva. The Saperda larva is attacked while boring the horizontal portion of its gallery. One parasitic larva is found on each host larva. The cocoon spun by the former prior to pupation, may be discovered in the portion of the tunnel which the latter had completed before its death.

From the comparatively small number of cocoons found, it did not appear that this Ichneumon was very common in this area. Throughout the investigations no instances of fungus-parasitism were observed either on adults or larvae. In the province of Gerona, Spain (17), however, an Entomophagous fungus has recently been found destroying both adults and larvae of this Longicorn.

In a note on the "Planting of poplars at Kininvie," Banffshire, Scotland, published in the *Transactions of the Royal Scottish Arboricultural Society*, of January, 1919, attention is drawn to the fact, that the cultivation of poplars for economic use has been very much neglected in this country in the past, and that the question of their cultivation is as yet in the experimental stage. It is certain, however, once the possibilities of the various species as economic forest trees have been definitely proved, that they will be more extensively planted in the future. Of all the more importance, then, both to forester and nurseryman, is the intensive study of this possible deadly enemy.

In conclusion it is with great pleasure that I acknowledge the advice, encouragement and facilities granted me by Dr R. Stewart McDougall in the carrying out of this work.

I am also indebted to Miss Clark, artist, Edinburgh, for the painting of the two coloured figures.

I particularly wish to express my thanks to the Carnegie Trust for the Universities of Scotland, for grant to cover artist's fee and cost of the reproduction of the figures.

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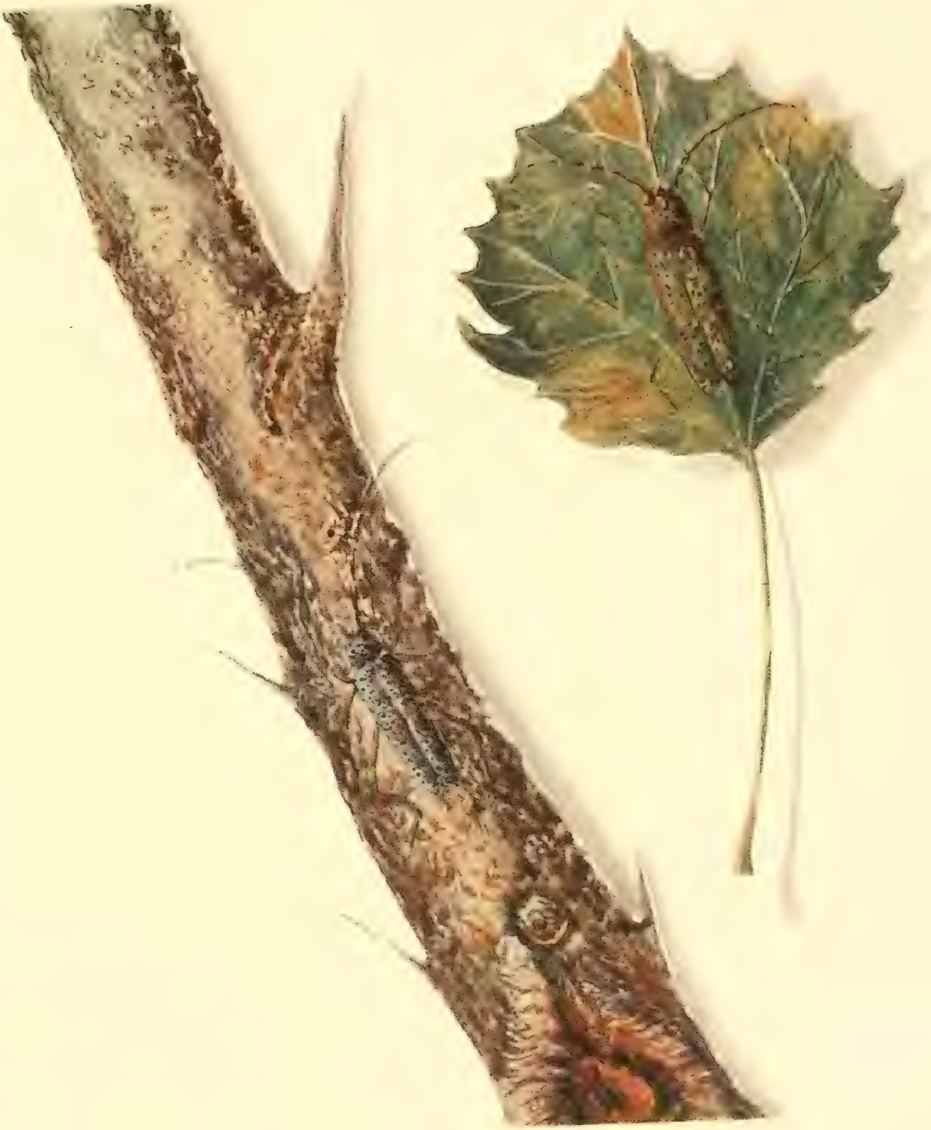
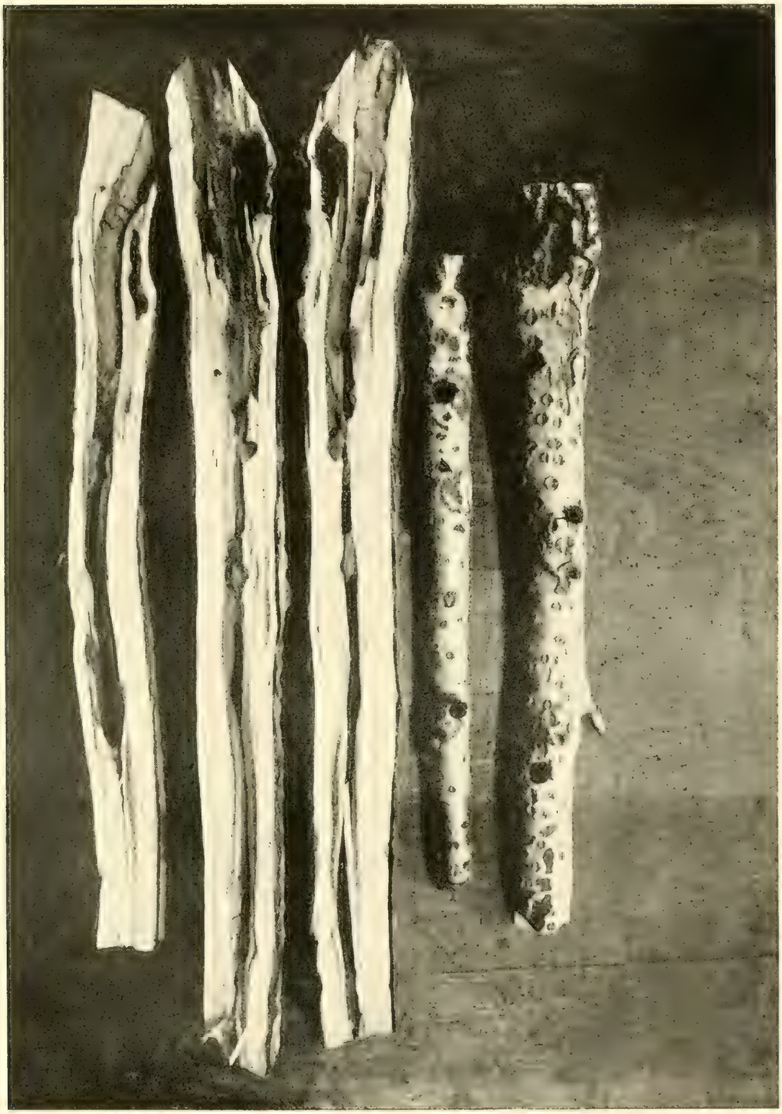
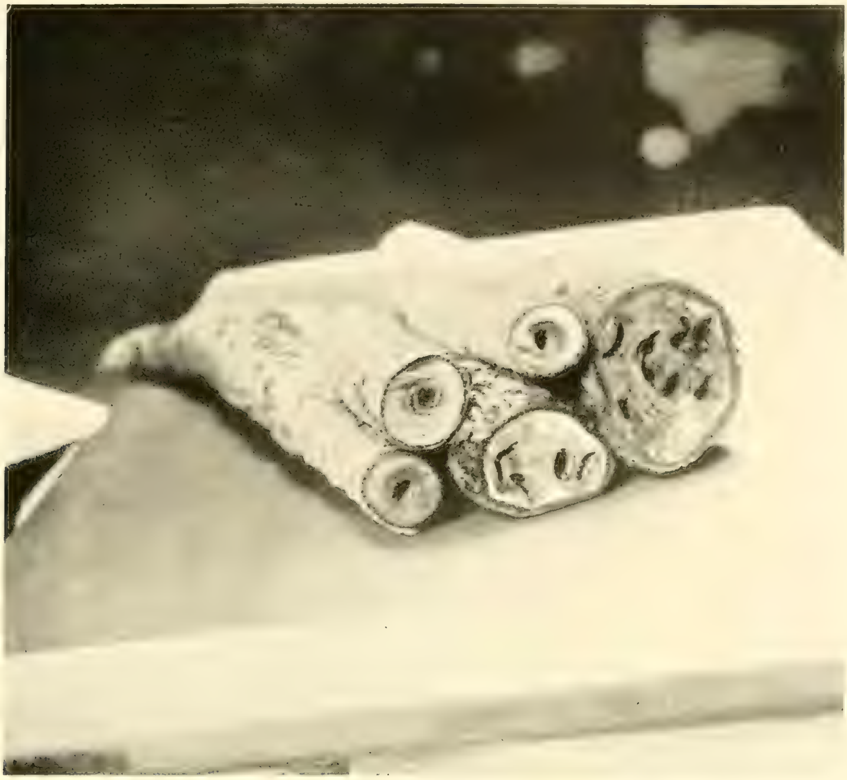


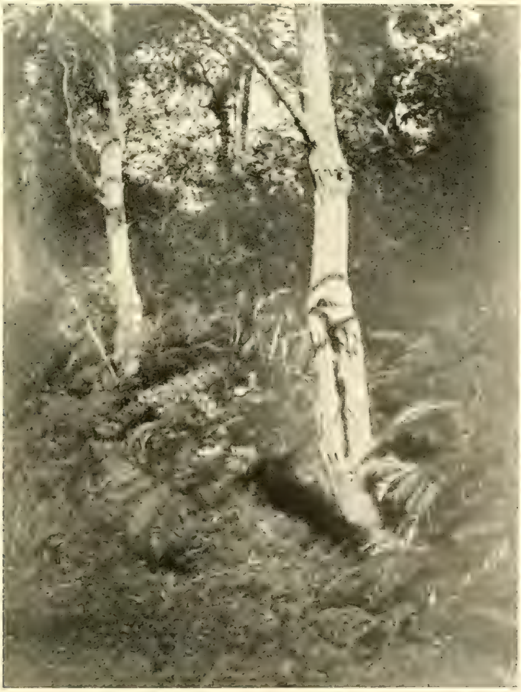
On the left: *Saperda carcharias* Linn., male (ash-grey variety) at rest on a twig of *Populus tremula* Linn.

On the right: *Saperda carcharias* Linn., female at rest on a leaf of *Populus tremula* Linn.

The figures illustrate how the colouration of the beetles is to some extent effective as a means of concealing them.







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DESCRIPTION OF PLATES.

PLATE XX.

On the left: *Saperda carcharias* Linn., male (ash-grey variety) at rest on a twig of *Populus tremula* Linn.

On the right: *Saperda carcharias* Linn., female at rest on a leaf of *Populus tremula* Linn.

The figures illustrate how the colouration of the beetles is to some extent effective as a means of concealing them.

PLATE XXI.

10–12 year old infested stems showing flight holes of adults above, and tunnels o larvae below. The flight holes are round in shape.

PLATE XXII.

Transverse sections of poplar stems badly tunnelled by larvae of *S. carcharias.* The diameters of the sections are as follows: lower row, left to right, 1″, 3″ average, 4″ approx. Upper row, left to right, 1¾″, and 1½″ approx. Tunnels in centre of sections average in diameter ¾″.

PLATE XXIII.

Stem of 35 year old poplar, showing fissuring of bark consequent on earlier attack by larvae of *S. carcharias.*

REVIEW.

Insect Pests and Fungus Diseases. By P. J. FRYER. (Cambridge University Press, 1920. 45*s*. net.)

A book dealing somewhat exhaustively with the pests, zoological and fungoid, ot fruit and hops, with the requisite attendant mechanical and chemical appliances and their use in combating them. The whole design of the work is evidence of the author's intent towards its practical use by cultivators, as evidenced by the classification of the material therein contained into headings embracing every detail for rapid reference. It is also happy in not pre-supposing that every grower has found time or inclination for the possession of knowledge on entomology or plant structure.

There are subtleties with regard to insects of economic importance that must be left for elucidation by the entomological expert, and translated by him into broad methods of treatment for the grower, who ever considers control before nomenclature and details; nevertheless accuracy is worth something for its own sake, and the entomologist, as such, will not be disposed to overlook the much useful information for the practical man contained in this book, because of such things as the common wasp being termed *Vespa crabro* and there being some originality in insect classification under the heading of "scientific."

The chemical side, with apparatus, is quite adequately dealt with in a most useful way, and there are calendars and tables, including capacity and quantitative estimation results, that cannot fail to be of value.

The work is full of illustrations, some coloured. A number of those derived from the camera are likely to prove a useful aid to identification of the subjects with which they deal, but the same cannot be said of the reproductions from drawings, which detract from the appearance of the work, which in this respect requires to be again judged by the counterbalance of other matter.

In a second edition the author would find it an advantage to do some re-editing in collaboration with an entomologist.

It should have been noted above that this review has been made solely from the entomological standpoint.

R. S.

VOLUME VII FEBRUARY, 1921 No 4

NOTES ON A CESTODE OCCURRING IN THE HAEMOCOELE OF HOUSE-FLIES IN MESOPOTAMIA.

BY J. H. WOODGER, B.Sc.

Assistant in Zoology, University College, London,
sometime Protozoologist in the Central Laboratory, Amara.

(With 3 Text-figures.)

1. INTRODUCTION.

THE parasite briefly described in the following notes was first observed by me in the course of a series of dissections of house-flies undertaken in conjunction with Capt. P. A. Buxton, R.A.M.C., in Amara, Mesopotamia, with a view to discovering to what extent the house-fly was responsible for the carriage of dysentery in that region. The results of this dysentery work have been published by Capt. Buxton elsewhere.

2. MODE OF OCCURRENCE IN THE FLY.

It was noticed one day, on opening the abdomen of a fly, that a number, about fifteen, of milky, globular bodies, apparently unconnected with the organs of the insect, poured out into the saline in which the dissection was being carried out. From the small amount of material obtained it is not possible to say more than that the parasite occurred free in the abdominal haemocoele.

3. LOCALITIES IN WHICH INFECTED FLIES WERE FOUND.

Flies were taken for this work from near British and Indian hospital latrines; from Arab compounds in and near Amara; from a village known as Deffas, about 2½ miles above Amara town, on the right bank of the Tigris; and from what may be described as the "dirty end" of the Amara bazaar.

As this parasite was not found in any of the flies from British or Indian latrines these localities need not be considered further. They were kept clean under the supervision of the sanitary sections of the R.A.M.C.

The remaining localities mentioned were, for the most part, in a very filthy state. The Arab compounds and villages were usually packed with live-stock—horses, cows, dogs, fowls, sparrows, rats, and lizards—and their excreta—all providing ideal conditions for the breeding of flies and the transmission of parasites.

The "dirty end" of the bazaar was open to the sky and crowded with the stalls of Arab vendors of meat, vegetables, and sweetmeats; it was always swarming with flies, but live-stock was, of course, very much less in immediate evidence than in compounds and villages.

4. SEASON AND INCIDENCE.

It will be seen from the table below that the dissections of flies from the regions mentioned were continued from March 9, 1918, until September 26, 1918, with breaks during May and August. It will be noticed at once that flies infected with the cestode were only found during the month of April. After the 30th of that month frequent examination of flies from the same localities failed to yield a single parasite.

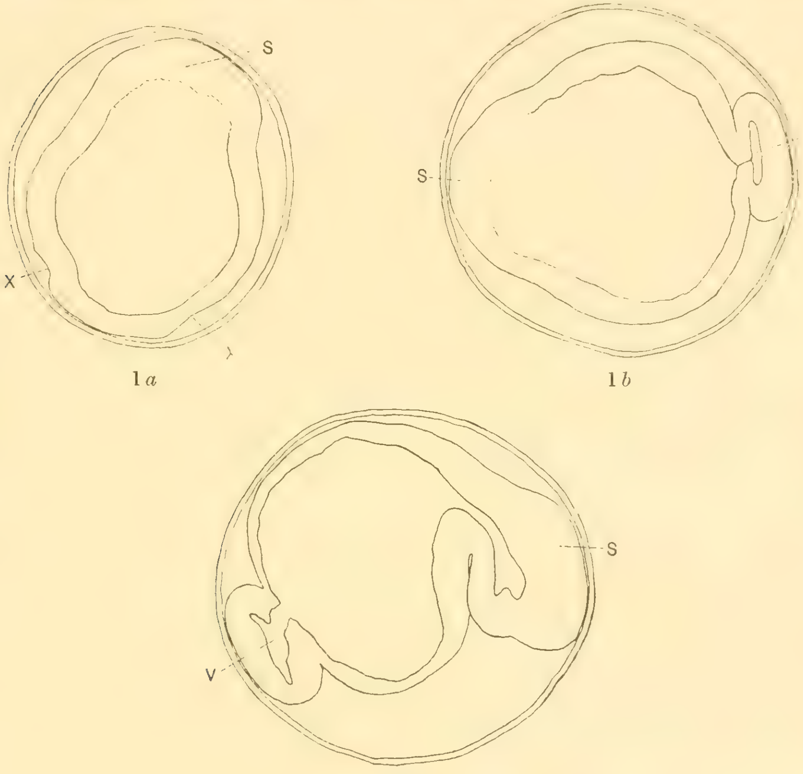
Table of Examinations.

	Number of flies examined			
Date 1918	Male	Female	Locality	Result
March 9	—	7	Bazaar	Nil
„ 26	9	6	„	Nil
„ 28	—	1	Deffas	Nil
„ 30	15	4	Compound near Amara	Nil
April 2	23	19	Bazaar	2 flies infected. Sex not recorded
„ 3	11	8	Compound near Amara	Nil
„ 17	—	7	Deffas	Nil
„ 18	—	21	„	Nil
„ 23	—	17	Compound in Amara	1 female fly infected
„ 24	—	15	„ „	1 female fly infected
„ 25	—	11	„ „	Nil
„ 29	—	14	„ „	Nil
„ 30	—	11	„ „	1 female fly infected
June 8	—	3	„ „	Nil
„ 15	—	10	„ „	Nil
„ 20	—	20	„ „	Nil
„ 21	15	15	„ „	Nil
„ 24	10	14	„ „	Nil
July 6	—	10	„ „	Nil
Sept. 18	—	4	„ „	Nil
„ 21	—	13	„ „	Nil
„ 26	—	25	„ „	Nil

The total number of infected flies found was only five out of the 338 dissected from the localities mentioned (*i.e.* all except British and Indian latrines),—a percentage of nearly 1·5 per cent.

5. Description of the Parasite.

The following description and accompanying figures are taken from live specimens examined fresh in saline. Three developmental stages are represented, the specimens of each being from different flies, since all the parasites from the same fly were found to be in approximately the same stage. All figures magnified approximately 145 times.



1 *a* 1 *b*

1 *c*

Fig. 1 *a*. The parasite in Stage I: *S*, scolex, *X*, points at which constrictions are appearing.
b. Parasite in Stage II: *S*, scolex, *V*, vesicle.
c. The same parasite, drawn one hour later.

Stage I. Fig. 1 *a* represents the earliest stage seen. The cyst-wall enclosing the embryo appears to consist of a single transparent, gelatinous envelope. The embryo itself consists of a thick-walled vesicle in which two distinct poles are recognisable. At one pole, *S*, destined to form the scolex, the wall is very thick, and its inner margin is difficult to make out, as is indicated by the dotted line. The other pole is distinguished, not by any striking difference in its wall, but by the signs of the beginning of a constriction at the points marked *X*.

During life slow waves of contraction are continually passing over the animal and consequently its shape may change very considerably. Fig. 2 is intended to illustrate this point, Fig. 2 *b* being drawn from the same specimen as Fig. 2 *a*, after an interval of three minutes.

Stage II. This is figured in Figs. 1 *b* and 1 *c*. These two figures also are drawn from a single specimen at different times, Fig. 1 *c* being drawn one hour after Fig. 1 *b*.

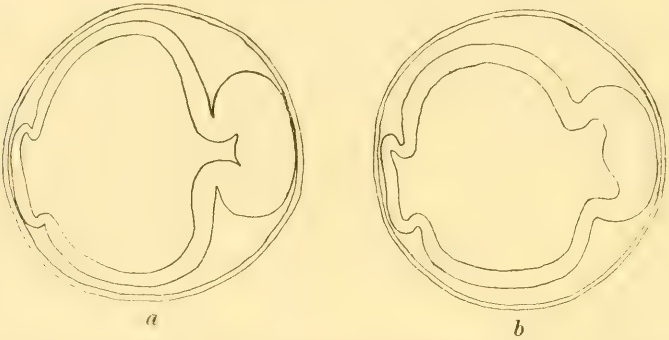


Fig. 2 *a*, *b*. Two drawings of another parasite, to show waves of contraction, taken with an interval of three minutes between them.

In the latter figure it will be noticed that the scolex-pole is little different from that of Fig. 1 *a*, but the constriction observed in the latter has now deepened so far as almost to separate off a flattened vesicle *V*. The cyst itself has increased somewhat in size.

After one hour we see, in Fig. 1 *c*, that the pole carrying the vesicle *V* is little altered, but at the opposite pole a thick-walled, club-shaped "head" is now marked out and folded over to one side. Remembering what has already been said concerning the rhythmical contractions of the animal it will be realised that it is difficult to say how far this difference between the scolex-pole of Fig. 1 *b* and of Fig. 1 *c* was due to these contractions or to an actual advance in development.

Stage III. This is represented by two parasites from one fly drawn in Fig. 3.

The entire cyst has now increased considerably in size. The vesicle is entirely separated from the parasite. The head, attached by a narrow neck to the somewhat shrunken bladder, bears four suckers and a club-shaped rostellum, armed with a single row of small hooklets.

It will be noted that there are certain differences between the two specimens figured in Fig. 3. The hooklets are smaller and more numerous in one than in the other; and the shape of the rostellum is also different in the two specimens, but this is probably merely the effect of different conditions of contraction. The separated vesicle *V* also is smaller in one than in the other.

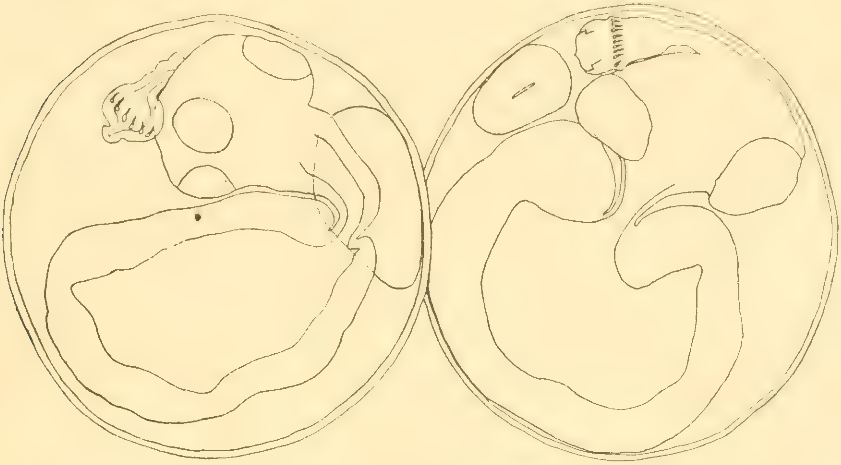


Fig. 3. Two mature cysticercoids (Stage III) from the same fly; with vesicle lying free in cavity of cyst.

6. FEEDING EXPERIMENTS.

With such a small amount of material very little could be done in the direction of experimentally infecting a vertebrate host, but the few experiments that were tried are perhaps worth mentioning.

On April 2, 1918, some fresh cysts were introduced by means of a pipette into the gullet of a lizard (*Ophiops elegans* var. *meizolepis*). The animal died on the 6th of the same month, probably as a result of too much exposure to the sun; examination of intestine and faeces revealed nothing.

On April 23 a similar attempt was made to infect two other lizards of the same species, also with negative results.

On April 24 some fresh cysts were introduced into the gullet of a young rabbit. Twelve examinations in the course of 25 days of the faeces of the rabbit, after shaking up with saline and centrifuging showed no cestode ova or any other sign of infection.

Equally negative results attended the attempt to infect a frog (*Rana esculenta*).

7. LITERATURE AND CONCLUSION.

In the literature of the Cestodes I have been able to find mentioned but two species for which the house-fly is claimed as the intermediate host. Both of these occur in chickens; they are: (1) *Choanotaenia infundibuliformis* (Goeze 1782) Raillet 1896, and (2) *Davainea cesticillus*.

With regard to Choanotaenia the account of the development of this species is contained in a much quoted paper of Grassi and Rovelli (4) in which they write, after remarking upon the wide distribution of this species, which they call *Taenia infundibuliformis*—"La ragione si è che l' oste intermedio è la Mosca (*Musca domestica*). Noi abbiamo nella sua cavita addominale trovati varie volta da 2 a 30–35 cisticercoidi, il cui scolice è identico a quello della *T. infundibuliformis*.* Nello stesso laboratorio della Universita di Catania, dove tenevamo molto materiale di Tenie dei Polli per i nostri esperimenti, abbiamo potuto accertarci che alcune Mosche si erano infettate."

They give one small figure of the cysticercoid which bears a rough general resemblance to that in my figure 3, but neither the envelope nor the vesicle *V* is shown, and the rostellum appears to be very small or in a very completely retracted condition.

In another paper (3) in which this species is mentioned Grassi and Rovelli merely state that the intermediate host is the fly and that the cysticercoid lacks a "tail," such as occurs in *Dipylidium caninum*, and which is perhaps represented in my species by the vesicle *V*, in Figs. 1 *b* and 1 *c*.

Stiles (6) gives a detailed account of the adult of *Choanotaenia infundibuliformis* under the name of *Drepanidotaenia infundibuliformis* (Goeze 1782), together with a long list of synonyms. On p. 45 he states: "Were it not for the fact that the original host (chickens) is known, I have the most serious doubt whether it would ever be possible to recognise this form; and whether even the numerous specimens recorded from chickens as *T. infundibuliformis* are to be considered as such is, in my opinion an open question." On the same page he also states: "as for the supposed life-history, with the fly as intermediate host, although I am not willing to deny the correctness of the hypothesis, I do insist that it is only an hypothesis...."

Detailed descriptions of the adult of this species will also be found in Ransom (5) and Cohn (2).

As to *Davainea cesticillus*, the second species I have mentioned, J. E. Ackert (1), in a preliminary communication, has described experiments in which he succeeded in infecting young chickens by feeding them on flies that had themselves been fed on the eggs of this tape-worm. He figures the hexacanth embryo but not the cysticercoid.

It will be seen therefore that it is impossible to identify my cestode with either of the above from the stages I have described. At the time my observations were made no literature bearing on the subject was available, and the possibility of the fowl being the definitive host was not considered.

It is hoped in publishing these notes that they will direct attention to the occurrence of this parasite in Mesopotamia and that they may be of assistance to anyone who is in a position to pursue the matter further.

I wish to express my thanks to Professor R. T. Leiper, D.Sc., M.D., for much help and criticism in the preparation of these notes for publication; and to Capt. P. A. Buxton for the use of material found in the course of his own dissections, and for constant assistance in the examination of experimental animals.

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ON CARRAGEEN. *CHONDRUS CRISPUS.*

By PAUL HAAS and T. G. HILL.

Botany Department, University College, London.

(With 5 Text-figures.)

The scarcity of gelatine during the period 1915–1919, and in many cases its poor quality, led those concerned to seek for a substitute, with the result that carrageen once more came back to favour. In this respect Mrs Maitland Malcolm was most active; the Ministry of Food expressed its approval of "Irish moss" in the preparation of invalid foods, and its collection was organised by the Food Production Department. The observations made by various members of the British Red Cross Society have thus led to a revival of interest in the plant, and at the instance of Professor Oliver we undertook its examination. It has been considered desirable to publish this preliminary general account for the use of those concerned not with the chemistry of the substance but with its value as food and in the arts, and to reserve for a future occasion our observations, as yet incomplete, on the more purely scientific aspects of carrageen.

Chondrus crispus, Lyngb., is a member of the Gigartinaceae, a family of the Florideae (red seaweeds), and is widely distributed on rocky sea shores. In the British Isles it is abundant on the west coasts of Ireland and Scotland and on the south and north-west coasts of Wales. In England it is reported from the south-west—Dorset, Devonshire, particularly the south coast, Cornwall and Somerset—and from North Yorkshire and Northumberland. It extends from three-quarters tide level to below low water mark and favours sloping localities, especially where the rocky shore gently slopes to low water mark.

Chondrus crispus is a perennial plant which reaches its maximum vegetative development in spring and summer. It is characterised by a tufted habit, the fronds, narrow, flat and stalk-like basally, branching distally into flat or curled expansions, varying in colour from purple brown to red purple in more strongly illuminated situations. Iridescence is a characteristic feature. The reproductive organs are immersed in the fronds.

The form of the plant shows much variation in the breadth and branching of the fronds, according to the conditions of growth, exposure to waves and surf for example. Four typical forms are shown in the accompanying figures, which were drawn by Miss Matilda Smith from specimens in the Kew Herbarium.

The "Irish moss" of commerce consists of the dried yellowish brown fronds of *Chondrus crispus* mixed with some *Gigartina mamillosa* (Fig. 5). The weed is collected at low tide and is spread on shingle or grass where it is cured by watering with either fresh or salt water and bleached and dried by exposure to the sun.

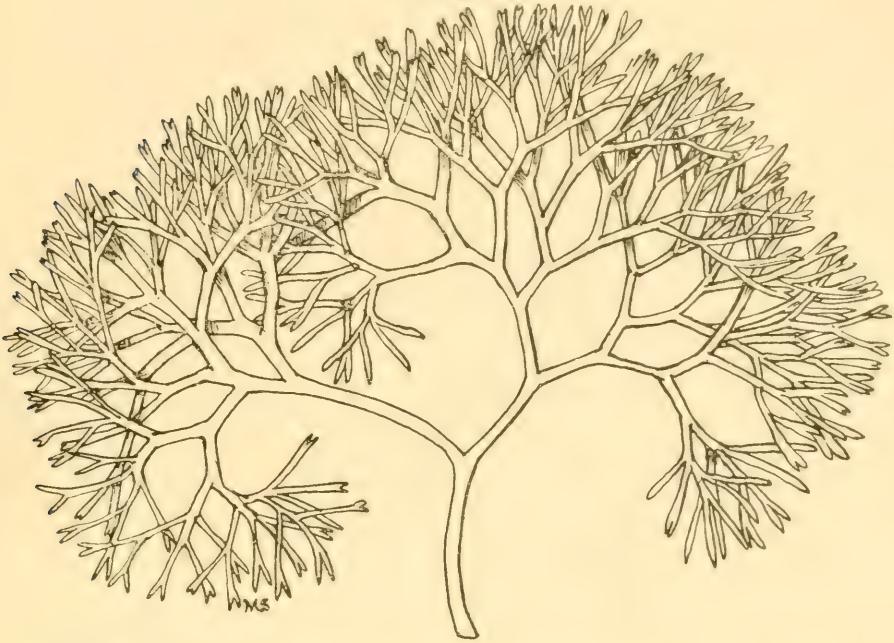

Fig. 1. *Chondrus crispus*. Narrow form from swift channels and rough water. (Nat. size.)

The wholesale price varies from £30–£90 per ton according apparently to the fancy of the dealer.

Uses of Irish Moss.

Irish moss or carrageen when boiled with water swells up and gives a gelatinous mass; on straining this yields a more or less transparent viscous solution which gelatinises on cooling. This material has been used in medicine as a demulcent and has by some been considered to be a specific for bronchial and other pulmonary complaints. In invalid cookery carrageen has been used in the making of jellies, but in ordinary domestic cookery it has hitherto been rarely used except in places where it naturally occurs[1]. In pharmacy it is employed as an emulsifying agent for oils, and it is also employed for fining beer, more especially in America; in the arts it is further used as a substitute for size in the

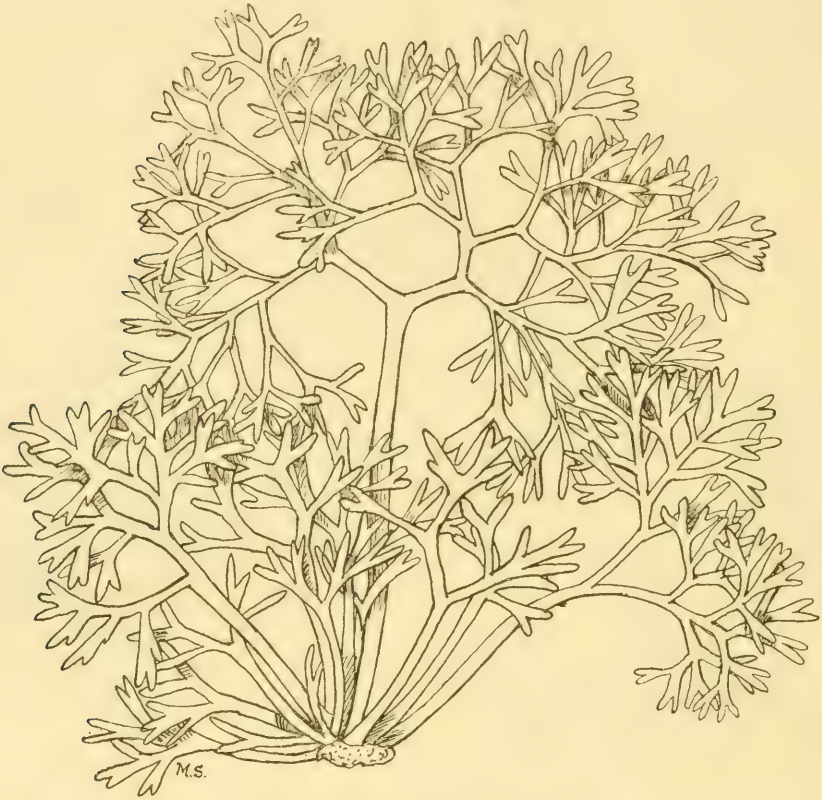

Fig. 2. *Chondrus crispus.* Narrow form from pools on open coast or roughish water which is well aerated. (Nat. size.)

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[1] Mrs O'Connell of Clifden, Connemara, informs us that only the better class folk in the west of Ireland use it as a substitute for gelatine while the peasantry do not even know of its value. The statement found in the literature that Irish moss is extensively used in Ireland as a food for human beings is therefore not borne out by this information; on the other hand, according to Mrs O'Connell, carrageen jelly and skim milk yields excellent results in the dietary of calves. See also Harvey, *Phycologia Britannica*, vol. III, London, 1846–51.

manufacture of paper, in the finishing of textiles[1], for thickening pigments and in the making of plaster for walls.

METHOD OF EXTRACTING THE GELATINISING SUBSTANCE.

The dried weed as received from the collectors was handpicked, foreign algae and other matter being removed; the material was then rapidly rinsed in two changes of distilled water so as to remove adhering dust and sea water salts. The fronds swell much in fresh water and solution of the gelatinising substance immediately begins; it is therefore essential, if an undue loss is to be avoided, for this preliminary washing to be carried out as rapidly as possible. After rinsing, the plants were squeezed free from excess of water, spread on clean paper and allowed to dry at room temperature and finally in the steam oven. To prepare the water-soluble gelatinising material two methods of extraction were employed:

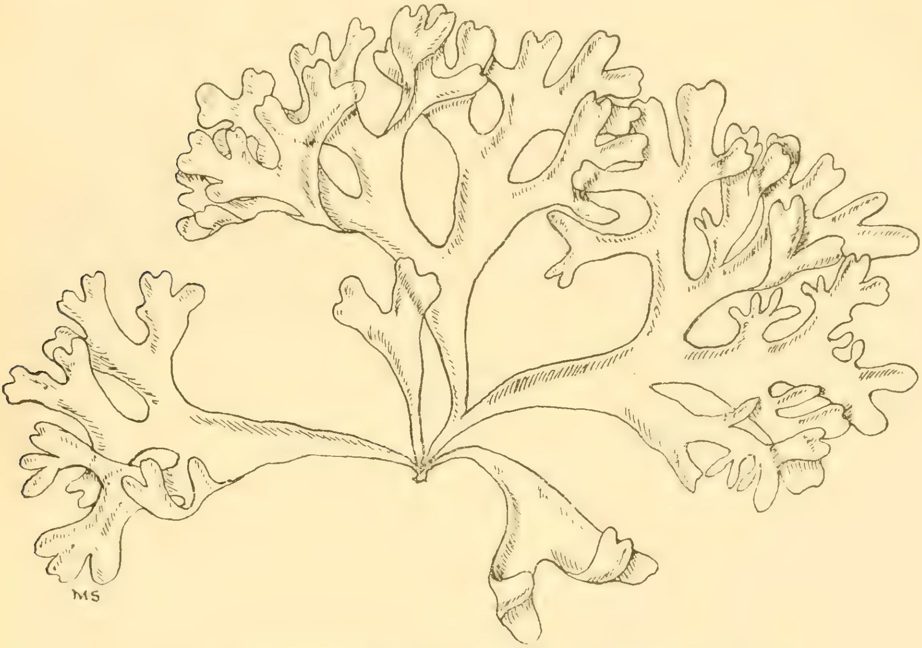

Fig. 3. *Chondrus crispus.* Medium form from fairly calm water. (Nat. size.)

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[1] See *The Textile Recorder*, 1919, p. 404.

(i) *Extraction with hot water.*

The powder was sprinkled on hot distilled water contained in a beaker flask heated on a boiling water bath and thoroughly stirred to prevent the formation of lumps. Sufficient powder was added to make roughly a 1 per cent. solution. After heating for half-an-hour, the contents of the beaker were filtered under pressure first through linen and then through filter paper in a Buchner funnel. The residue was repeatedly extracted in this way and the combined filtrates were then poured on to a shallow tinned copper dish and heated over a boiling water bath. When dry the carrageen extract peeled off.

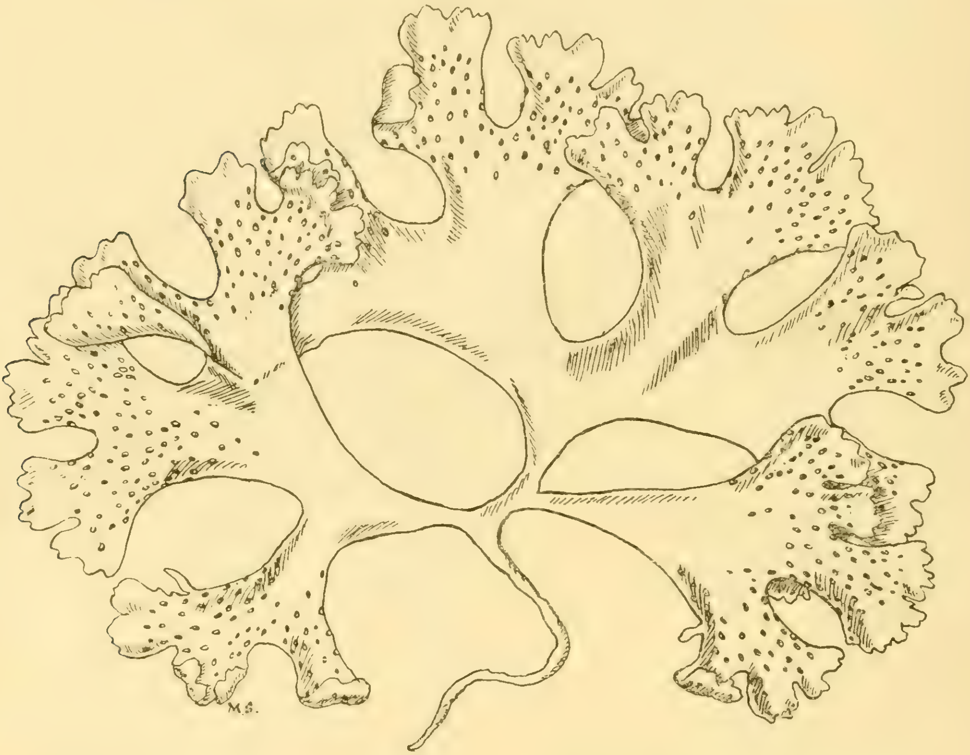

Fig. 4. *Chondrus crispus.* Broad form grown under quiet conditions on shallow shores, harbours, and muddy bays. (Nat. size.)

By this method 70–75 per cent. of water-soluble extract may be obtained.

(ii) *Extraction with cold water.*

The powder was stirred into cold distilled water and after the addition of a little toluene was allowed to stand for 12 hours, with occasional stirring; the supernatant solution was then syphoned off, filtered and evaporated; more distilled water was then added to the residue and the process repeated.

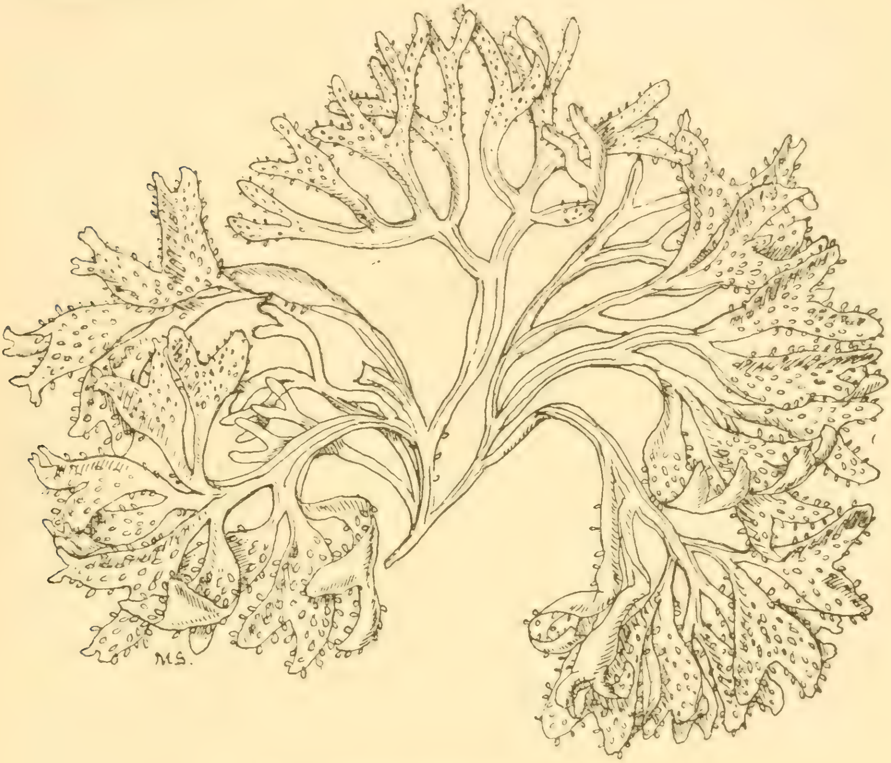

Fig. 5. *Gigartina mamillosa.* (Nat. size.)

With a view to comparing successive fractional extracts each portion was evaporated separately.

Exhaustive extraction by means of cold water as above yielded only 18·85 gms. of water-soluble material from 40 gms. of the ground weed in 36 days.

Whether extracted by hot or by cold water, the appearance of the scale carrageen is a clear gelatine-like substance of a pale dull yellow colour, brittle when quite dry, which apparently keeps well for an indefinite time. Although of similar appearance, it has been found that the scale carrageen extracted with hot and with cold water differs in certain physical characters, notably the rapidity of solution in water, hygroscopic properties, viscosity of their aqueous solutions and the behaviour of such solutions towards Rochelle salt.

Action of Rochelle salt. Rochelle salt (sodium potassium tartrate) has a marked effect upon the gelatinising of solutions of carrageen too weak to form a gel under ordinary conditions; thus 5 c.c. of a 1 per cent. solution of a *hot water* extract of carrageen boiled with five drops of a 20 per cent. solution of Rochelle salt sets to a gel on cooling whereas a 1 per cent. solution of a *cold water* extract is not gelatinised by boiling with Rochelle salt.

This indicates that carrageen contains more than one colloidal substance extractable by water, one of which is more soluble in cold water than the other and this has an important bearing on the mode of preparation of the extract, since a cold water extract is deficient in one of the constituents which may be extracted by hot water.

GELATINISING POWER.

The best method of gelatinising scale carrageen is to soak the material first in water: a rapid absorption takes place accompanied by considerable swelling; solution is effected quickly if the vessel be placed in water heated to about 60° C. As compared with gelatine and agar, carrageen occupies an intermediate position. Both gelatine and carrageen dissolve easily in water at relatively low temperatures; agar, on the other hand, requires prolonged heating at about 90° C. The melting point of agar is correspondingly high, while the melting points of gelatine and carrageen are relatively low. There is a marked difference between these last two substances with regard to the sharpness of their melting points: whilst gelatine passes from the solid to the liquid state with some degree of suddenness, carrageen on melting yields a viscous liquid which unlike gelatine remains thick while hot, and this fact makes it hard to say exactly at what temperature the jelly melts. For this reason Hatschek's method, which works well for gelatine, is consequently not altogether suitable for carrageen and the figures given below obtained by this method are therefore only approximate.

The accompanying table gives the approximate melting points obtained for equivalent strengths of gelatine and carrageen (hot extract):

	Gelatine	Carrageen
3 %	27·7° C.	27–30° C.
5 %	29·5° C.	40–41° C.

From these figures it will be seen that whereas the melting point of a 3 per cent. solution is approximately the same for both substances, the melting point of a 5 per cent. solution of carrageen is considerably higher than that of a 5 per cent. gelatine, and that, so far as physical properties are concerned, a 5 per cent. carrageen could be used for slope or plate cultures, without fear of liquefaction in incubators at or slightly above blood heat.

The only published observations on the melting points of carrageen which we have been able to trace are those of Standford[1] who compared the gels obtained from various seaweeds with gelatine. He gives the melting point of a 3·2 per cent. solution of gelatine as 15·5° C. and that of a 3·6 per cent. solution of carrageen as 21° C. These figures are markedly different from those recorded above; it is, however, impossible to examine them critically since Standford gives no information regarding his methods.

The gelatinising property of carrageen is not destroyed by boiling; thus a 3 per cent. aqueous solution of carrageen boiled for 3½ hours under a reflux condenser sets on cooling after a few minutes whereas a 3 per cent. gelatine solution similarly treated does not set for several hours.

HYGROSCOPIC PROPERTIES.

The dried plant and also the scale preparations of the aqueous extract of the plant are markedly hygroscopic. Very varying figures may be obtained according to the atmospheric moisture obtaining at the time of the experiment.

For the air-dried weed figures varying from 2·54–18·2 were obtained. Other authors give varying figures; thus Church[2] found 18·78 per cent. of moisture in the air-dried plant, Jolles[3] 12·36 per cent. of moisture, and in Thorpe's *Dictionary of Applied Chemistry* the value 17·9 per cent. is given.

In order to compare the hygroscopic properties for hot and cold water extracts of the weed determinations were carried out concurrently on these materials with the following results.

Cold water extract	23 %	moisture
Hot water extract of residue ...	19 %	,,
Direct hot water extract of weed	21 %	,,

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[1] Standford, *Pharm. Journ.* 1884, XIV, 1010.

[2] Church, A. H., *Journ. Bot.* 1876, XIV, 71.

[3] Jolles, M. and A., *Just. bot. Jahresber.* 1896, II, 452.

It may be remarked that the accurate determination of hygroscopic moisture is a matter of some little difficulty owing to the fact that the material when dried to constant weight in a steam oven may show signs of darkening and decomposition at or about the final stage.

ASH CONTENT.

Carrageen contains a relatively high percentage of ash both in the plant and in the scale: in the latter instance the amount varies according to the method of preparation, the earlier fractions of cold water extracts yielding the greatest amounts. The following are typical analyses:

A. The untreated plant gave 14·6 per cent. ash.
B. Scale carrageen:

(i)	Cold water extract	5th fraction gave 27·07 per cent. ash. 10th fraction gave 24·32 per cent. ash. 30th fraction gave 21·50 per cent. ash.
(ii)	Hot water extract of residue remaining after more or less complete extraction with cold water	gave 16·30 per cent. ash.
(iii)	Hot water extract. (Plant extracted with hot water only)	gave 22·70 per cent. ash.
(iv)	Residue from (iii)	gave 5·19 per cent. ash.

Church gives 14·15 per cent. of ash in the dry plant, Flückiger and Hanbury[1] found that the aqueous extract of the plant and the plant itself contained more than 15 per cent., Czapek[2] gives 20·6 per cent., Flückiger and Obermaier[3] found 16 per cent., whilst Jolles found but 1·59 per cent. This last result is obviously incorrect, but the mistake may be due to a displacement of the decimal point.

It was found impossible to remove the mineral constituents by dialysis, a fact commented on by previous authors; indeed in one instance an increase of ash on dialysis was found to obtain[4]. For our own part we found that dialysis of a solution of scale carrageen extending over a period of nearly a month in running water reduced the ash from 22·79 per cent. to but 20·55 per cent.

That this reluctance to dialyse was not due to any peculiar attraction of the colloidal material for salts was shown by the fact that a solution of scale carrageen could be entirely freed from added sodium chloride or sulphate by two days' dialysis.

Initial treatment of the solution with dilute hydrochloric acid in the cold or with dilute sodium carbonate followed by filtration and dialysis also failed to have the desired effect.

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[1] Flückiger and Hanbury, *Pharmacographia*, London, 1874.

[2] Czapek, *Biochemie d. Pflanzen*, II, 818.

[3] Flückiger and Obermaier, *Schwerz. Wochens. Pharm.* 1868, XIII.

[4] Moeller and Thoms, *Real Enzyklopädie d. gesammten Pharmazie*, 1900, III, 382.

Subsequently it was found that the amount of sulphate which is precipitated from an aqueous solution of the extract is very much greater after hydrolysis with dilute acids than before such hydrolysis; this observation may account for the difficulty experienced in removing the ash constituents by dialysis.

NITROGEN CONTENT.

Both the weed and the product obtained from it by extraction with water give positive reactions for proteins with concentrated nitric acid and with Millon's reagent, but the glyoxylic acid reaction for tryptophare is not given by either.

Estimations of nitrogen in the dried weed and the various extracts gave the following figures:

A. Dried plant	1·93 %
B. Scale carrageen:	
(i) Cold water extract	·99 „
(ii) Hot water extract of residue from (i)	1·09 „
(iii) Direct hot water extract	·82 „
(iv) Residue from (iii)	4·82 „

The figures given by previous authors for the nitrogen content of the plant are: Jolles 2·08 per cent., Flückiger and Obermaier 1 per cent., and Thorpe[1] 1·5 per cent.

HYDROLYSIS.

The use of carrageen as a food naturally leads to the examination of its behaviour under the action of various hydrolytic agents. The work of others has shown that the water extract of carrageen is a polysaccharide which is converted into various sugars by the action of strong mineral acids[2], but from this it does not follow that carrageen can be hydrolysed by the agents it normally encounters in the human or in the animal system. For this reason many experiments were carried out with solutions of scale carrageen in order to find out the effect of relatively weak hydrolytic agents. In all cases the presence of reducing sugars after the reaction was taken as a positive result: controls always were employed and due precaution taken to guard against bacterial action. Since scale carrageen gives a slight acid reaction, its solution was rendered neutral or alkaline when appropriate.

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[1] Thorpe's *Dictionary of Applied Chemistry.*

[2] Our observations on this aspect of the subject are reserved for a future occasion.

Ptyalin. Undiluted filtered saliva and diluted saliva, obtained by washing out the mouth with distilled water, gave positive results when incubated at 50° C. for several hours, especially when the medium was strongly alkaline. At body temperature the results after 12 hours were either negative or very feebly positive.

Extract of pancreas. Negative results both at 37° C. and 50° C.

Hydrochloric acid. A 0·2 per cent. solution of hydrochloric acid was employed so as to have an acidity approximating to that of the gastric juice. A slight positive result was obtained after three hours' incubation at 37° C. In the same period a much stronger reaction obtained after incubation at 50° C.

Citric acid. A 5 per cent. solution acting for two hours at 37° C. gave a similar result to that obtained with 0·2 per cent. hydrochloric acid at 50° C. Heated on a boiling water bath for a few minutes with 5 per cent. citric acid carrageen loses its gelatinising power, and the solution acquires a strong reducing action to Fehling solution. The difficulty experienced in making shapes of carrageen flavoured with lemon juice is thus accounted for by the hydrolytic action of the acid.

The above observations suggest that the carbohydrate portion of carrageen is likely to be but slightly affected by the digestive juices of the human body[1] and that the value of carrageen as a food resides in its physical rather than in its chemical properties. The favourable results observed after its use in invalid diet, judging from the published recipes for various dishes, are due to the other ingredients—sugar, milk, eggs, etc.—rather than to the carrageen which provides a pleasing vehicle: moreover when it is borne in mind that the strength of the jelly is rarely likely to exceed 5 per cent., the amount of carrageen consumed in such dishes would be insignificant.

In view of the modern interest in vitamines and the possibility of these substances being responsible for the favourable results recorded in the use of carrageen, Dr Drummond, of University College, kindly undertook the investigation of the material from this point of view; he reported that he was unable to find any traces of either of the fractions associated with vitamines.

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[1] The fact that cattle are capable of digesting cellulose by bacterial action in the intestine makes it impossible to express any views as to the digestibility of carrageen by cattle without special experiments.

FRIT FLY (*OSCINIS FRIT*) IN WINTER WHEAT.

By F. R. PETHERBRIDGE.

(*School of Agriculture, Cambridge.*)

In a previous article[1] the writer has given examples of bad attacks of this fly on winter wheat following leys containing either rye grass or Italian rye grass.

The following experiments show that this is due to the fact that the autumn brood of flies lay their eggs on the grass, and that the larvae feed on the shoots, and after the grass is ploughed in, they eventually migrate to the young wheat plants.

In 1917 a bad attack of frit fly was noticed on one part of a field of wheat on the University Farm, whereas the other part of the field was practically free from attack.

The following shows the differences in the previous treatment of these two pieces of wheat.

Part A. Badly attacked by Frit Fly.
Crop in 1916—*Italian rye grass and red clover.*
Ploughed November 3rd, 1916.
Little Joss sown November 10th, 1916.

Part B. No Frit Fly attack.
Crop in 1916—*Red Clover.*
Ploughed October 10th, 1916.
Little Joss sown October 23rd, 1916.

As a result of this and other observations, an experiment was arranged to see if the ploughing in of the rye grass before autumn would prevent an attack of frit fly.

In 1917 a piece of trefoil and Italian rye grass was divided into three plots.

Plot A was ploughed on July 12th,
cross ploughed on July 14th.
Cultivated from August 26th onwards.
Harrowed on September 26th.
Drilled on October 3rd.

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[1] *Loc. cit.* vol. IV, Nos. 1 and 2, September 1917.

Plot B Fed off by sheep.
Ploughed on October 1st,
then harrowed,
and drilled on October 3rd.

Plot C Fed off by sheep.
Ploughed on November 1st,
then harrowed,
and drilled on November 3rd.

The results observed were as follows:

Plot A. Although I made several careful searches I did not find a single plant attacked by frit fly.

Plot B. Fairly bad attack of frit fly. About 10 per cent. of the plants attacked.

Plot C. This plot was damaged by birds, so that it was difficult to estimate the amount of damage, but many frit larvae were found.

This experiment was repeated in 1919–1920 with a view to determining when the frit fly larvae migrate from the rye grass into the wheat.

Before ploughing in the autumn the Italian rye grass was examined and found to be very badly attacked by frit fly larvae, which were feeding on the young shoots. The intensity of the attack was probably increased by the ploughing up of over 90 per cent. of the rye grass in summer and thus leaving a much smaller amount of grass in which the flies could lay eggs.

Plot A. Crop in 1919—Italian rye grass and trefoil.
Ploughed July 25th.
Wheat drilled October 30th.

Very few frit larvae found in wheat. A few also found in Italian rye grass plants not ploughed under. A few plants attacked by wheat bulb fly.

Plot B. Crop in 1919—Italian rye grass and trefoil.
Ploughed November 7th.
Drilled November 20th.

About 25 *per cent. of the plants attacked by frit larvae.* A few plants attacked by wheat bulb fly.

Plot C. Crop in 1919—Rye and vetches.
Folded with sheep.
Wheat drilled in July, 1919.

A few frit fly larvae found. A few wheat bulb fly larvae attacking wheat and couch (*Agropyrum repens*).

Plot D. Crop in 1919—Mangolds and cabbages.
Wheat drilled November 20th.

No frit fly larvae found. Fairly bad attacks of wheat bulb fly in patches.

Plot E. Crop in 1919—Mangolds, swedes and turnips.
Wheat drilled December 18th and 19th.

No frit fly larvae found. Fairly bad attacks of wheat bulb fly in patches.

In the above experiments the only loss of crop from frit fly was after Italian rye grass ploughed in during the autumn. The ploughing in of the rye grass before harvest (*i.e.* bastard fallowing) prevented a loss of wheat from the attacks of frit fly.

On Plot B tufts of buried rye grass were dug up during the winter and examined for frit fly larvae at intervals of about a month.

On January 7th a large number of frit fly larvae were present in the rye grass, and many of the shoots were not decayed.

On February 6th a few frit larvae were found to be attacking the wheat plants, but large numbers were still present on the rye grass.

Throughout February and March the attack on the wheat gradually became worse, whereas the number of larvae in the rye grass gradually became fewer. April 7th was the last date on which frit fly larvae were found in the buried rye grass. By this date much of the rye grass was decayed, but a few shoots seemed to be suitable as food for the larvae.

POT EXPERIMENTS.

These experiments were carried out in 5 inch pots in the laboratory.

No. of Pot	Procedure	Remarks
1	Tuft of rye grass (dug up from Plot B) containing frit fly larvae buried in soil in pot. Wheat sown February 16th	2 plants attacked on March 16th 9 plants attacked on April 17th
2	9 frit fly larvae from buried rye grass placed near seedling wheat plants on February 6th	3 plants attacked on March 26th
3	Small pieces of rye grass containing 6 frit fly larvae buried near seedling wheat plants on February 2nd	3 plants attacked on March 26th
4	8 frit fly larvae from buried rye grass placed near seedling wheat plants on February 9th	2 plants attacked on March 3rd
5	7 frit fly larvae from buried rye grass placed near seedling wheat plants on February 16th	3 plants attacked on March 26th
6	4 frit fly larvae from buried rye grass placed near seedling wheat plants on February 2nd	1 plant attacked on March 26th
	2 more added on March 3rd	3 plants attacked on April 1st
	1 more added on March 25th	
		Examination of the attacked plants showed that the damage in all cases was due to frit fly larvae

No flies hatched out from these pots. An examination of the attacked plants showed that some of the larvae died before pupation. The single pupa which was found was parasitised.

Of the cases of winter wheat attacked by "frit fly" which I have examined during the last few years, nearly all have been after a ley containing one of the rye grasses ploughed up during the autumn.

On a farm in Norfolk only one field of wheat after rye grass had escaped. This was ploughed up in the middle of August, whereas the fields which were attacked were ploughed up much later.

In Cambridgeshire I found a piece of wheat slightly attacked, following a crop of turnips, but in this case the land was very foul with couch (*Agropyrum repens*) and other grass weeds, so that it is quite probable that the eggs were laid on these.

The only other exception was after a crop of white clover, where it is probable that grasses were present with the clover, although not sown.

I have never seen any appreciable reduction in crop from an attack after potatoes, beans, corn or fallow, but it seems probable that if after either of these the land was covered with grass weeds during the early autumn, the wheat following might be attacked. I have often seen wheat after the above crops free from attacks when neighbouring fields were attacked.

The damage done by the frit maggot seems to be more on a loose tilth than on a compact tilth. In the former case a larger percentage of plants die, probably because they do not tiller so quickly as on firmer soils. Fields in good condition suffer less than those in poor heart probably for a similar reason.

These experiments and observations prove that the frit fly larvae present in the rye grasses are capable of migrating to and damaging wheat plants after the grass is ploughed in.

They also show that an attack of frit fly on winter wheat following rye grass may be avoided by bastard fallowing. Wheat after a bastard fallow, however, is very liable to a bad attack of wheat bulb fly (*Leptohylemyia coarctata*), although in the above experiments this pest did very little damage after this method of procedure.

SOME REMARKS ON THE METHODS FORMULATED IN A RECENT ARTICLE ON "THE QUANTITATIVE ANALYSIS OF PLANT GROWTH."

By R. A. FISHER,

Chief Statistician, Rothamsted Experimental Station.

In the *Annals of Applied Biology* has appeared a paper (4) by Briggs, Kidd and West; according to the authors "The series of articles of which this is the first instalment, constitutes an attempt to formulate methods for the quantitative analysis of plant growth and to apply these methods to data which have been lying dormant in the literature for forty years."

That the paper here criticised is primarily concerned with the methods by which primary observations are to be treated in the study of plant growth is emphasised by a reference made to it in an earlier paper (3) in the *New Phytologist.* "*The Relative Growth Rate, R,* is the weekly percentage rate at which the dry weight increases. It may be assumed for purposes of calculation that the increase from week to week takes place exponentially, *R* being the exponent, or that it takes place linearly. Both are approximations. As to the relative merits of the two different methods the reader is referred to (4)."

It will be noticed that no definition is here given of the *Relative Growth Rate, R,* except for the case in which the mass increases exponentially, when this is so

$$m = m_0 e^{Rt} \quad \text{.................................(I)}$$

where m is the mass and t the time, and R may be calculated from any two observations:

$$R = \frac{\log m_2 - \log m_1}{t_2 - t_1} \quad \text{........................(II),}$$

where the suffixes 1 and 2 indicate the first and second observations.

This is the quantity termed the *Efficiency Index* by Blackman (1), and which may be correctly termed the *Relative Growth Rate*; we shall use the latter term. No indication is given above as to what meaning is to be attached to the term *Relative Growth Rate* when it is assumed that the increase takes place linearly or as to how it is to be calculated from the observations.

It is here fitting to remark that whatever assumptions are made as to the variations of growth rate with time, the relative growth rate *at any instant* is necessarily

$$\frac{1}{m}\frac{dm}{dt}=\frac{d}{dt}\log m \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{(III)};$$

the value of R, calculated by formula II, therefore gives correctly the average value of the relative growth rate over the period between the two observations, whatever may be the nature of the changes in relative growth rate over this period. This property of formula II, and the precise definition of relative growth rate at any instant given by III should be borne in mind in considering the confused and contradictory use of the term in the ensuing quotations.

For when we refer to the paper under discussion (4) to ascertain what are the two methods of calculation, the merits of which are to be discussed, we find that the term relative growth rate is now applied to a quantity calculated as a schoolboy is taught to calculate Simple Interest. The justification of this procedure must be quoted in full ((4), p. 104).

> There are various methods of presenting the results, and in the first instance we shall use the relative growth rate curve. The principle of the proposed method of expressing rate of growth is analogous to that of the method by which the rate of most reactions, both chemical and physiological, are expressed, namely amount of change per unit of material per unit of time. Since the amount of material in the growing plant is constantly changing, and since the relative rate of growth is not constant, as the following analysis will show, to achieve mathematical accuracy, the increase should be measured over an infinitely short period. This procedure is manifestly impossible, and as we have no exact knowledge of the way in which the relative rate of growth varies, over a given period we have adopted the following purely conventional method of defining relative rate of growth. The relative rate of growth of a plant during any given week of its life-cycle, is the amount of dry matter which 100 gms. of dry matter taken at the beginning of the week adds during the week. A week has been chosen since this is the usual interval between determinations of dry weight in most experiments on growth in plants. It must be noticed that the method does not pretend to mathematical accuracy, being merely an approximate average for the week, but with such results as are at present available nothing more accurate can be obtained."

The most striking feature of this paragraph is the contrast between the precision of the first definition of relative growth rate contrasted with the inconsequent arbitrariness of the method proposed for its calculation. Nothing could be more clear than to define relative growth rate as "amount of change" (*i.e.* increase) "per unit of material per unit of time"; the statement is equivalent to that of expression III. But why, if so precise a definition can be given of the quantity we wish to measure, should we be reduced to measuring it by a "purely conventional method" which "does not pretend to mathematical accuracy?" The reasons given for this falling away are quite inadequate. It is true that "to achieve mathematical accuracy," in determining the rate of growth at any instant, "the increase should be measured over an infinitely short period": it should also be measured with infinite accuracy, and on an infinite sample of plants. But the discussion being devoted to the quantitative analysis of such data as Kreusler supplies, it is not clear what would be gained if we could determine the relative growth rate with mathematical accuracy at any one instant. The environmental data quoted by Briggs, Kidd and West are the *Mean Temperatures* for the week, and in some cases the total hours of sunshine. Both of these may be regarded as mean values of quantities which vary in an unknown manner during the week. The corresponding quantity which we require for comparison with them is the mean value of the relative growth rate, which is given with mathematical accuracy by formula II. The difficulty of obtaining the relative rate of increase with high accuracy at any instant thus hardly justifies the complaint that "nothing more accurate can be obtained" than a "purely conventional method," which in fact introduces errors up to 100 per cent. or more!

For the Simple Interest formula employed

$$100 \times \frac{m_2 - m_1}{m_1(t_2 - t_1)} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{(IV)}$$

is extremely inaccurate in relation to the data to which it is applied. The principal cause of this inaccuracy is that the dry mass of the active plant is assumed to have throughout the week that value that is assigned to it at the beginning of the week. It often happens that during the week the mass has more than doubled; in such cases the relative rate of increase is much exaggerated by reckoning the increase on the initial mass. This error has nothing to do with the assumption of linear increase, for if the rate of increase during the week be assumed to be linear, the mean value of the mass for this period will be

$$\tfrac{1}{2}(m_1 + m_2)$$

and the rate of increase reckoned on this mean mass, gives a much better approximation. The formula obtained in this way

$$100 \times \frac{2(m_2 - m_1)}{(m_1 + m_2)(t_2 - t_1)} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{(V)}$$

is compared with that of Briggs, Kidd and West in the following example ((4), p. 107).

Date of harvest	Mass	IV	V	II
June 1st	·268 gm.			
		108	70·4	73·5
,, 8th	·559			
		91	62·7	64·8
,, 15th	1·069			

Column IV shows the values given by Briggs, Kidd and West, column V the values obtained from the approximate formula V, which would be appropriate for the assumption of linear increase[1], column II gives the true values of formula II; for comparison all are written as percentages. It will be observed that in the first instance IV is 34·5 in excess of the true value, while V is 3·1 in defect, in the second instance IV is 26·2 in excess, and V is 2·1 in defect. The greater part of the error in IV is due to reckoning the increase upon the initial mass.

The errors produced in this way are very irregular; for positive values the rates of increase are exaggerated, for negative values they are made unduly small; so that if in one week the mass is diminished, and in the second it is increased to its former value, the rate of decrease calculated by formula IV will be smaller than the rate of increase which has exactly counterbalanced it. For very small values the formula is approximately accurate. Applied to such data as those presented its irregularities render it most unsuitable for statistical treatment.

But another irregularity is introduced by Briggs, Kidd and West. In the words of a footnote ((4), p. 105), "Where results are not given for a week, we have calculated the increase per 100 gms. for the period, and divided the result by the number of weeks in the period." Such a procedure would indeed be accurate, if the true measure of relative rate of increase had been chosen. Its effect upon the growth rate as estimated by formula IV may best be shown by recalculating the growth rate in the above example, ignoring the value of June 8th. Then for the whole fortnight:

		Relative rate of increase per week		
Date of harvest	Mass	IV	V	II
June 1st	·268 gm.			
		149·4	59·9	69·2
,, 15th	1·069			

The average weekly rate of increase for the fortnight as calculated by the principles of Simple Interest is thus much greater than that of either of the weeks composing it. The value given by formula V, though not so ridiculously discordant, shows that the error of this formula increases rapidly as the time interval is increased, that of formula III alone gives a concordant result, being the mean of the values of the two component weeks.

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[1] In the case of linear increase, the relative growth rate necessarily diminishes, having its highest value at the beginning and its lowest at the end of the period. Column IV then shows the value at the beginning, V the value at the centre of the period, and II, in this as in other cases shows the mean value over the whole period.

This example brings out a point in the utility of II which is worth noting. It illustrates the fact that growth rates calculated by II may be expressed at once in any unit of time, irrespective of the intervals employed experimentally. In general it is most suitable to use the day as the unit, and for this purpose the values in column II need only be divided by 7. For the values of IV a dilemma arises; according to the method of correction quoted above, they also should be divided by 7, although this would lead to values inconsistent with any possible daily increases in weight; the only self-consistent method would be to reckon the interest payable daily on the principles of compound interest, and this if performed by the use of logarithms amounts to calculating the value of column II from that of IV, dividing by 7, and then finding the corresponding value of column IV. This process should be in itself of considerable educative value in the study of these different methods of measurement.

These being the facts, it remains to enquire how it was that with Blackman's work before them, and knowing that the efficiency index had been successfully applied (2), the authors of (4) chose to employ so inaccurate a method of calculation. The point is dealt with in the following passage ((4), p. 106).

> "It might be suggested that allowance could easily be made for the continuous increase in dry weight during the week by assuming that this takes place at a uniform rate, and consequently that by means of the following logarithmic formula the rate could be determined:
>
> $$\log W - \log W_0 = \dot{r},$$
>
> where W is the dry weight at the end of the week, and W_0 the dry weight at the beginning of the week.
>
> In curve A, Fig. 1, this allowance has been made. In curve B, the ordinates are relative growth rates calculated by our method, that is, without making allowance for the continuous increase during the week. The curves show similar variations of growth rate from week to week. The more complicated method, however, does not achieve accuracy, as it rests on the assumption that the rate remains constant during the week, an assumption manifestly incorrect since the rate varies from week to week. Both methods are purely conventional and only approximate to accuracy, and nothing definite is to be gained by adopting the more complicated procedure."

At first sight one might judge from this paragraph that the two methods of calculation had been judged to be practically equivalent by an inspection of the diagram referred to, but a glance at that diagram is sufficient to show that this cannot be so, for while the disagreement is inconsiderable for the periods of slow increase or decrease, at the time of most rapid growth the formula ultimately adopted is approximately double the true value; whence it must be apparent that any quantitative study of the growth rates is materially influenced by the choice of the measure of growth rate. Nor can the difficulty of calculation explain the choice, for with the aid of a table of natural logarithms the correct value is more quickly calculated than any of its approximations; indeed it is surprising that the experience of calculating one series did not bring conviction on this point. One can only explain the choice by the mistaken impression, which is emphasised above, that the use of the logarithmic formula involved the assumption that the relative rate of increase is independent of the time; an assumption which as the authors state, is manifestly incorrect.

This conclusion is confirmed by an apparently disconnected discussion, with which the paper opens, of the general mathematical formulae which have been suggested to represent the growth history of annual plants; among them there is ascribed to Blackman the view that this growth history can be represented by an exponential curve, that is to say, by a constant relative growth rate. Whether this view of the growth history of annual plants has ever been advocated, I am unable to say, but there can be no doubt that in advocating the use of accurate methods for measuring relative growth rate, Blackman (1) is amply justified.

SUMMARY.

The methods of calculation formulated by Briggs, Kidd and West for the analysis of plant growth are inaccurate, (i) in introducing a large exaggeration when the plant is increasing in mass, (ii) in applying to periods of varying length a method of calculation which thereby becomes self-inconsistent.

The correct measure for the mean value of the relative growth rate over any period, long or short, is that advocated by Blackman under the name of the "efficiency index."

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THE INFLUENCE OF SOIL FACTORS ON DISEASE RESISTANCE.

By ALBERT HOWARD, C.I.E.

Imperial Economic Botanist, Pusa, India.

(With 5 Text-figures.)

I. Introduction.

One of the features of the modern literature on agricultural science is the number of papers dealing with the diseases of plants in which insects and fungi are concerned. Much less attention, however, has been paid to disease and to the factors on which disease-resistance depends. It is now well understood that the unit species which go to make up the varieties of cultivated crops differ greatly among themselves in resistance to certain parasites and that in some cases at any rate this character can be inherited. Further, it is a matter of common experience that the various diseases only become epidemic where conditions assist the spread of the parasite and at the same time injuriously affect the condition of the crop which is being attacked. Briefly stated, the ravages of any parasite are found to depend on the kind of plant grown and on the conditions under which it is cultivated. We know practically nothing however of the reasons why one unit species is resistant to disease and why others, belonging to the same variety, do not possess this character to any great degree. Further, little has been done to trace the influence of separate soil factors on disease-resistance.

During the last 15 years, opportunities of growing the same crop in India under widely different conditions of soil and climate and of studying the distribution of the crops of this continent have been utilised. At the same time, many observations on the incidence of disease have been made and of the general conditions which appear to precede serious damage by parasites. In some instances, the matter has been carried further and an attempt has been made to ascertain what soil factors are responsible in lowering the natural resistance of a crop to attack. In practically every case, light has been thrown on the subject by a systematic examination of the root-system[1]. The results obtained are summed up in the present paper. They are admittedly incomplete but are put forward with a definite purpose, namely, to suggest that much more attention should be paid in future investigations of diseases to the general facts of root-development and to the condition of the absorptive areas of the root-system both before the actual advent of the parasite and during the period when the disease is actually established. Up to the present, attention has been paid chiefly to the influence of soil-aeration and soil temperature on disease-resistance.

II. SOIL-AERATION.

The importance of the soil-aeration factor in the growth of crops has been obscured by several causes. In the first place, the chief agricultural experiment stations at which soil problems have been studied have been situated in humid regions where the soil obtains frequent applications of highly oxygenated water in the form of rainfall. In the second place, the discovery of artificial manures has influenced agricultural science just as profoundly as it has revolutionised practice. When most soils are found to respond at once to applications of combined nitrogen, phosphates and potash or of various combinations of these substances and when artificial manures are purchasable in any market place of the country, it is natural to regard such soil deficiencies as due to exhaustion and to find in applications of artificial manures the natural remedy. Under circumstances such as these no stimulus to the study of factors like soil-aeration is likely to occur. When, however, we push over cultivation into the desert and endeavour to make up for defective rainfall by irrigation which often produces impermeable crusts on the surface, the importance of soil-aeration soon becomes manifest[2]. Deprived of regular applications of dissolved oxygen in the form of rainfall, the crop and the soil have to rely on other means of obtaining new supplies of this gas and of getting rid of accumulations of carbon dioxide. Under such circumstances the physical condition of the soil takes on a new meaning and any cause which affects gaseous interchange between the pore spaces and the atmosphere is found to affect the crop immediately. Not only does soil-aeration influence the amount of growth but also the development of the root-system and the resistance of the crop to disease. In some cases defective soil-aeration actually causes disease.

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[1] *Agr. Jour. of India*, Special Indian Science Congress Number, 1917, p. 17.

[2] *Bulletins* 52–61, Agr. Research Institute, Pusa, 1915–16.

The wilt-disease of Java indigo and other monsoon crops. These wilt-diseases are examples of a definite disease in which parasites have not yet been shown to play a part.

Java indigo (*Indigofera arrecta* Hochst.), the species now generally cultivated in Bihar, frequently suffers from wilt during the late rains. At the beginning of the monsoon, growth is normal but in wet years a change takes place about mid-July in the character of the foliage while the rate of growth slows down. The leaves alter in appearance, assume a yellowish-green, slaty colour, become reduced in size and show extensive longitudinal folding. After this, leaf fall is rapid until only stunted tufts of foliage at the ends of the branches remain. In severe cases, this is followed by the death of the plant, the process taking place slowly, a branch at a time. The external symptoms of wilt suggest extensive root damage which is confirmed by exposing the root-system by means of a Knapsack sprayer. Wilted plants are found to possess very few fine roots and nodules in an active condition. The main tap-root and the laterals are alive and normal but the fine roots are mostly dead or discoloured and the number of absorbing root hairs is exceedingly small. The destruction of the active root-system including the nodules takes place from below upwards. When wilt is well established, the absorbing roots still alive are all in the upper two or three inches of soil. Evidently some factor is in operation which destroys the fine roots in the subsoil and which afterwards affects those towards the surface.

Other investigators have failed to find any parasite responsible for the trouble. No insects could be discovered attacking the fine roots and none of the well-marked appearances of fungoid attack were evident.

The association of extensive root damage with wilt suggested a detailed study of the roots. For this purpose, it was necessary to expose the root-system without damage including the absorbing areas and the nodules. This is easily accomplished in the fine silt-like soils of Bihar by means of a Knapsack sprayer. The range in the root-systems of the various types which make up the indigo crop was found to be as great as that of the above-ground portion of the plant. The mode of branching of the roots closely corresponded with that of the shoot. The type of rooting could always therefore be foretold from the mode of branching. The root-system in this crop is the mirror image of the shoot. Nodular development was found to be most intense at the break of the rains in May and June and to be most pronounced on the roots near the surface. Soil-temperature was found to affect the growth of roots and a distinct resting period ensued during the cold weather of December, January and early February. Of great interest were the results obtained when actively growing indigo plants were cut back. This was followed in all cases by the death of the fine roots and nodules and before new shoots were formed extensive root regeneration was necessary. The formation of new roots during the monsoon was found to be more rapid if there was a break in the rains after cutting back, and to take place much more readily in the case of surface rooted types than if the root-system was deep. The next step in the investigation was to determine whether wilt is actually caused by the gradual destruction of the fine roots and nodules as seemed probable. Wilt was produced experimentally in the following ways:

(*a*) By the mutilation of the root-system. One example of wilt produced in this manner may be quoted. An indigo plant was partially cut back on June 21st, 1919. On August 5th, the roots were exposed by the Knapsack sprayer and were found normal and healthy in all respects. Before replacing the soil, the fine roots and nodules on the laterals were removed to the depth of one foot but below this point the soil was not disturbed. Wilt rapidly developed and when the entire root-system was again exposed on August 29th very few active roots were found.

(*b*) By deep interculture, during the rains, of indigo sown in lines. Two well-marked cases of this have occurred at Pusa recently. In 1918, Java indigo, sown in double lines with wide spaces between to admit of interculture, speedily lost in vigour and developed much more wilt than the broadcast crop side by side which was not cultivated. In 1919, the experiment was repeated with four types of indigo sown on two different types of soil. The indigo grown in double lines with interculture yielded less crop and developed more wilt than the neighbouring broadcast plots which were not cultivated. The cultivation was found to destroy the lateral roots near the surface on which the plants were dependent at that period of the year.

(*c*) By October and November cultivation of old indigo, dependent for its crude sap on superficial roots. After the rains, the only active roots of an old indigo crop are quite close to the surface. If the land is cultivated these are destroyed and wilt develops. Mulching the surface with straw to preserve the moisture and to prevent these roots drying up as the season changes has the reverse effect.

(*d*) By cutting back young rapidly growing August-sown plants in October, when the reserve materials in the tap-root are insufficient for root regeneration. Cutting back at this period kills the majority of the plants but a few produce wilted shoots.

(*e*) By complete cutting back in the cold weather when the root regeneration of surface-rooted types is difficult probably on account of low soil-temperatures. In December, 1918, 641 healthy well-developed August-sown plants were cut back when over five feet high. The following February, 162 of these were badly wilted, 185 were partly wilted and 294 were normal. A number of root washings were made and in all cases wilt was found to be associated with the practical absence of root regeneration. The plants which developed wilt were those which had their laterals near the surface, the deeper rooted plants producing normal growth. Thus the monsoon results are reversed during the cold weather. In the cold season, the factor which checks root regeneration is apparently low soil-temperature. This affects surface-rooted plants much more than deep-rooted types. The plants were kept under observation till April by which time a remarkable change had taken place. The rise in the soil-temperature in March caused the wilted plants to recover, root regeneration took place and the growth became normal.

(*f*) By waterlogging slowly from below during the rains, by closing the drainage openings of lysimeters. At the beginning of the rains of 1918, indigo was sown in two sets of lysimeters. These were air-tight cemented tanks, 1/1000 of an acre in area, four feet high, built above the ground level and provided with drainage openings which could be closed at will. In one set, alluvial soil exceedingly rich in available phosphate (0·318 per cent.) from the Kalianpur Farm near Cawnpore was used, in the other light Pusa soil was employed. The latter, when analysed by Dyer's method, gives very low figures for available phosphate (0·001 per cent.). In both soils the indigo in the lysimeters with free drainage escaped wilt altogether. When the drainage openings were closed and waterlogging from below took place all the plants were wilted in both Kalianpur and Pusa soil. Wilt in the Kalianpur soil (rich in available phosphate) was much worse than in Pusa soil (low in available phosphate). The growth in Kalianpur soil was much slower than in Pusa soil.

These experiments establish the cause of wilt. The disease results from damage to the fine roots and nodules under circumstances where root regeneration is difficult or impossible.

As has been stated above wilt generally makes its appearance during the latter half of the rainy season. During this period it is often the cause of low yields of indigo. The agency which brings about wilt during this period has been found to be defective soil-aeration caused by the upward rise of the ground water, combined with the destruction of the porosity of the surface soil by heavy rain. This interferes with soil-aeration and produces root asphyxiation. Soon after the monsoon begins in June, the level of the rivers rise followed by that of the ground water. The movements of the river levels and the general ground water are illustrated by the curves shown in Fig. 1, which represent the state of affairs of the river at Pusa and of one of the wells (about a quarter of a mile distant) for the years 1910 and 1912.

The curves are typical of the subsoil water conditions of North Bihar

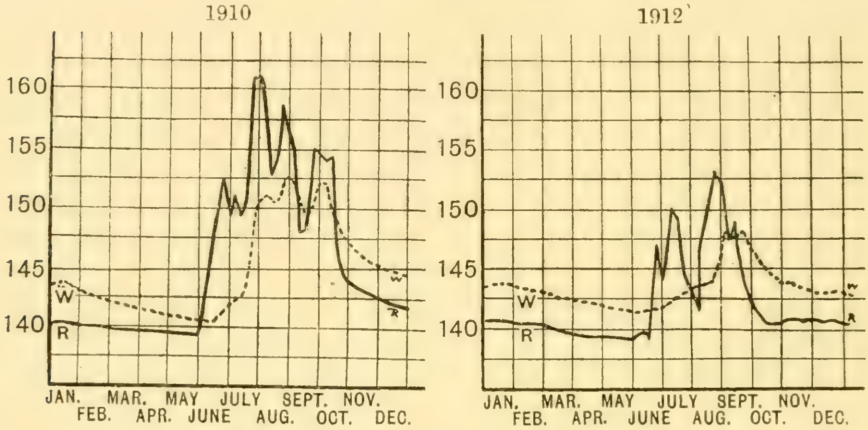

Fig. 1. Changes in the river and well levels at Pusa.
The well levels are shown by dotted lines. The observations are expressed in feet above mean sea-level.

Table I. *Percentage of CO_2 in the Soil Gas from three different plots in the Botanical Area, Pusa, in* 1919[1].

Month and date when the soil gas was aspirated and analysed	Plot No. 1, grassed down	Plot No. 2, grassed down but partially aerated by trenches	Plot No. 3, surface cultivated	Rainfall in inches since Jan. 1st, 1919
Jan. 13th, 14th and 17th	0·444	0·312	0·269	Nil
Feb. 20th and 21st	0·472	0·320	0·253	1·30
March 21st and 22nd	0·427	0·223	0·197	1·33
Apr. 23rd and 24th	0·454	0·262	0·203	2·69
May 16th and 17th	0·271	0·257	0·133	3·26
June 17th and 18th	0·341	0·274	0·249	4·53
July 17th and 18th	1·540	1·090	0·304	14·61
Aug. 25th and 26th	1·590	0·836	0·401	23·29
Sept. 19th and 20th	1·908	0·931	0·450	30·67
Oct. 21st and 22nd	1·297	0·602	0·365	32·90
Nov. 14th and 15th	0·853	0·456	0·261	32·90

[1] I am indebted to Mr Jatindranath Mukherji for these determinations.

during the rain. That the rise of the subsoil water combined with the consolidation of the surface soil does interfere with soil-aeration is shown by the periodic determination of the soil gases at Pusa during 1919 (Table I), a year when rainfall was below the average and when the movements of the ground water were very slight.

During this year, indigo wilt was almost negligible and only made its appearance at Pusa on two occasions, between July 23rd and Aug. 7th, and again between Sept. 1st and 23rd. A reference to Fig. 2 will show that these attacks followed a rise of the ground water combined with heavy rain. During these periods, the roots of many of the affected plants were exposed and compared with those of normal individuals. In all cases, most of the nodules and fine roots of the wilted plants were dead except a very few near the surface of the ground. The root tips of

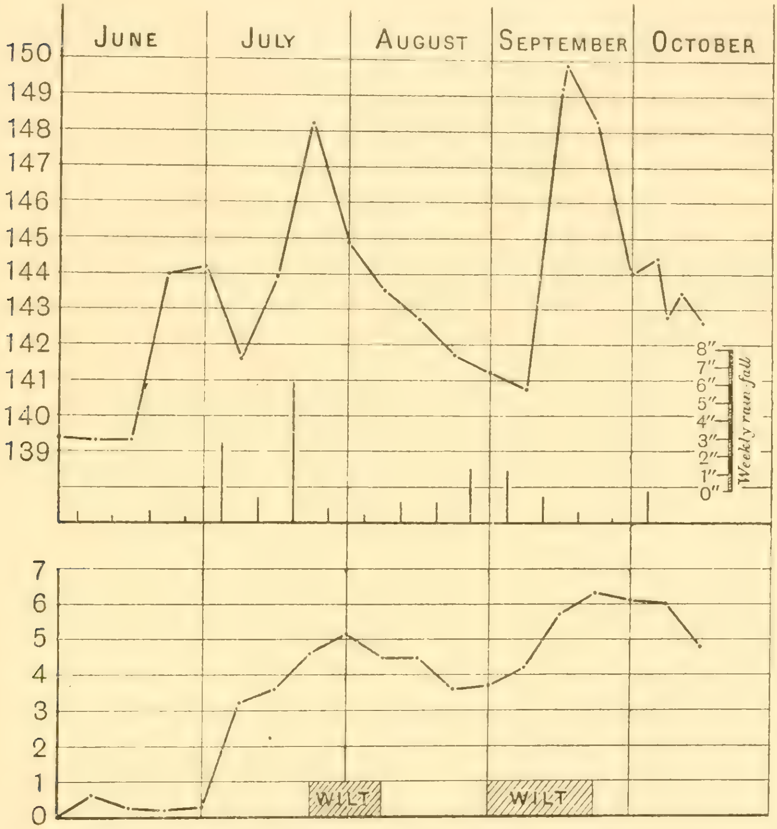

Fig. 2. Rise and fall of the river and well levels at Pusa in 1919.

normal plants exhibited marked aerotropism and were found to have turned upward towards the air. This continued until a break in the rains and a fall of the ground water restored soil-aeration when normal growth ensued.

Confirmatory evidence of the view that wilt during the rains is due to the destruction of the fine roots and nodules caused by poor soil-aeration has been obtained in several directions. The actual soil conditions under which wilt naturally occurs can be reproduced in a lysimeter by closing the drainage openings. The slow rise of the water-table leads to the destruction of the fine roots and nodules from below upwards and to the production of wilt. Recovery from monsoon wilt takes place in the lysimeters and also in the field after the aeration of the soil improves and when the temperature permits of the regeneration of the roots. Indigo grown on porous soil in other parts of India under a high rainfall, such as Dehra Dun and the Chattisgarh Division of the Central Provinces, escapes wilt altogether. In Bihar, wilt is always most severe in years of heavy rainfall when the subsoil water remains at a high level for long periods. It is negligible in years of short rainfall like 1919 when the rise of the subsoil water is very slight.

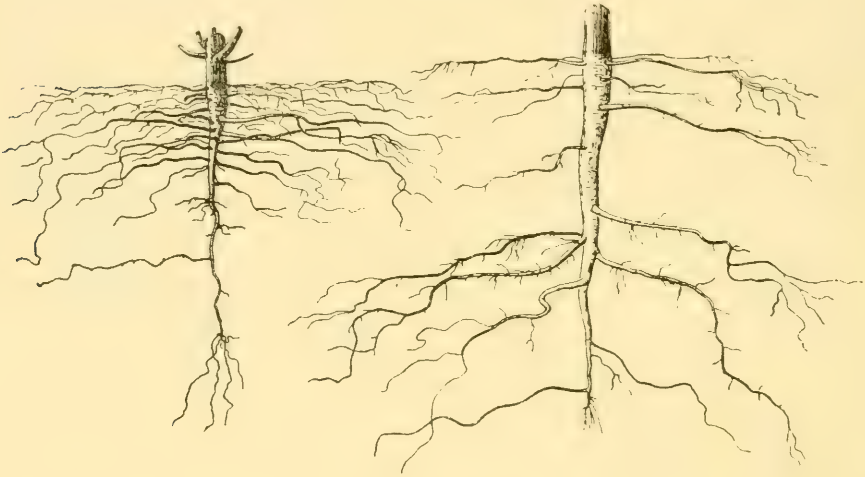

Fig. 3. The root-system of *Hibiscus Sabdariffa* (left) and *H. cannabinus* (right).

Wilt in Bihar during the monsoon is by no means confined to Java indigo. It is common on many deep-rooted varieties of "patwa" (*Hibiscus cannabinus* L.) and "sann" (*Crotalaria juncea* L.) while shallow-rooted types of these two species are little affected. Further, surface-rooted species like "Roselle" (*Hibiscus Sabdariffa* L.) thrive no matter how wet the monsoon may be. The roots of Roselle in wet years exhibit marked aerotropism leaving the soil and growing all over the surface of the ground. The differences between the distribution of the roots of Roselle and of deep-rooted types of *patwa* are shown in Fig. 3, while in Fig. 4 the roots of an early and late type of *patwa* are illustrated. The surface-rooted Roselle crop and the early types of *patwa* do well at Pusa even if the soil becomes waterlogged occasionally. The deep-rooted types in such seasons, on the other hand, suffer severely from wilt. In such cases, the fine roots are destroyed from below upwards and the details follow closely those already described in the case of Java indigo.

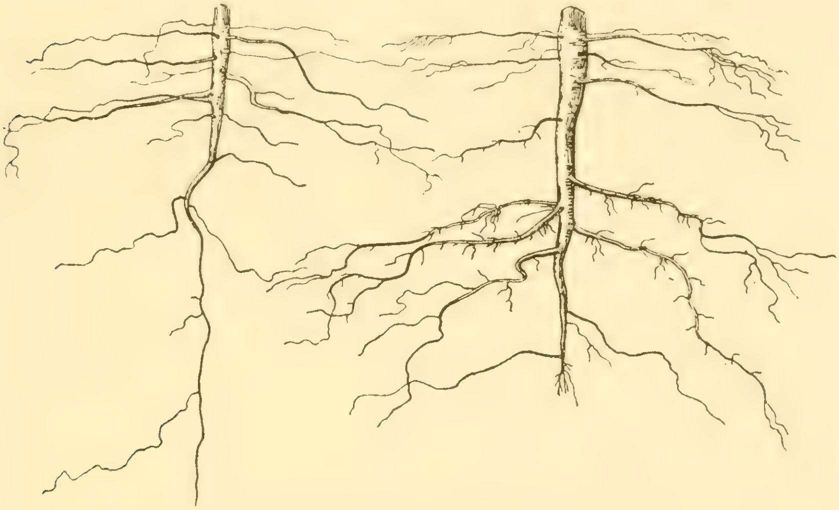

Fig. 4. Early (left) and late (right) types of root-systems in *H. cannabinus.*

Similar results have been obtained at Pusa in the case of two varieties of *sann* hemp (*Crotalaria juncea* L.). The local Bihar variety with surface roots sets seed but the deep-rooted tall variety from the black soils of the Central Provinces suffers from wilt and various insect diseases and hardly yields any seed crop.

The wilt diseases so far dealt with result from the slow destruction of the active root-system which follows the cessation of drainage and aeration during the rains. No parasite appears to be involved in any of these diseases. The remainder of this paper deals with diseases in which either insects or fungi are concerned, but in every case the actual attack follows the operation of some injurious factor such as poor soil-aeration, a high soil-temperature or increased humidity. All these cases require more detailed investigation which it is the object of this paper to provoke.

In connection with the investigation of the wilt disease of indigo and of *Hibiscus cannabinus*, some observations have been made on the conditions which appear to precede the attacks of two insects *Psylla isitis* Buckt. on indigo and the red cotton bug (*Dysdercus cingulatus* Fabr.) on *Hibiscus cannabinus*.

Psylla frequently attacks the stems and leaves of indigo leading to malformation and twisting of the growing points. Sometimes the attack stops at the end of the rains and the new leaves then become quite normal. Stems showing *Psylla* attack below and healthy foliage above are quite common and the attack does not spread to the new growth. It has been frequently observed at Pusa that applications of fresh undecayed organic matter (such as green manure) applied shortly before sowing as well as dressings of oil cake after sowing are always followed by severe attacks of *Psylla*. Examination of the root-system shows restricted and abnormal development and much discolouration of the active roots. The sequence of events is so well marked that the matter deserves to be studied in much greater detail. The fermentation of fresh organic matter in the soil seems to lead to changes in the sap and in the cells of the leaf which predispose the indigo plant to attack. In all cases we have examined, root discolouration precedes and accompanies the insect attack.

Equally interesting are the attacks by the red cotton bug on *Hibiscus cannabinus* at Pusa. These always follow the destruction of the fine roots and the onset of wilt. Year after year *patwa* grows normally during the early rains but when the wilt appears in September and October the plants attract swarms of the red bug. The wilt-free plots of Roselle in the neighbourhood are not attacked. Here again we appear to be confronted with a change in the cell-sap arising from root damage which prepares the way for the parasite.

The rusts of wheat and linseed. During the progress of the wheat experiments at Pusa, many hundreds of pure lines have been grown and in many cases the same cultures have been repeated year after year. In some instances, these pure lines have been grown in the field and also in flower-pots. In others, they have been grown immediately after the rains with or without a deep cultivation before sowing. Interesting differences between the amount of damage done by black rust (*Puccinia graminis* Pers.) to the same unit species in the same year have often been observed according to the way the plants were grown. In all cases, the individuals grown in flower-pots showed much less rust than the same unit species grown in the field and the difference was most marked. In flower-pots the roots of the wheat plants obtain a copious supply of air. This apparently increases the resistance of the plant, the rust colonies remain small and few in number and ripening of the grain takes place normally. When grown in the field, the aeration of the roots is reduced, the rust runs much more rapidly and the grain is often shrivelled. Similar differences in rust resistance are observed between plots of the same unit species when grown on heavy land with or without deep cultivation after the rains before sowing. The better the physical condition of the subsoil, the greater the rust resistance. This matter is being followed up further and the connection between rust attacks and the distribution and character of the root-system is being investigated at Pusa. Some interesting facts have already emerged. Several of the most rust-resistant wheats at Pusa are very shallow-rooted, some of the most rust-liable types from the black soils are exceedingly deep-rooted. Soil-aeration appears therefore to play an important part in the relations between the host and the parasite in rust attacks.

In the case of the linseed crop, the matter is being carried further. A large collection of the linseeds of India has been made at Pusa and the various unit species have been isolated and classified. The unit species fall into three groups according to the size of the seed and the character of the root-system. The linseeds of the black soils of Central India possess large seeds and a deep root-system which enables the crop to withstand the cracking of these soils. The types found in the plains have small seeds and a shallow root-system (Fig. 5). The third group is intermediate in all respects. When grown at Pusa in alluvial soil there is a great difference in the appearance of these groups of linseed. The small-seeded class is very luxuriant and does not suffer from rust and other diseases. The large-seeded deep-rooted class grows and sets seeds with difficulty. The plants appear starved and are often attacked by rust (*Melampsora Lini* Desm.). There is a very great difference in the appearance of the active roots of the deep-rooted types of linseed attacked by rust and the shallow-rooted types which escape this disease. The former appear starved and there is extensive discolouration. The latter are turgid, white and exceedingly vigorous.

Red rot of sugar-cane. One of the difficulties in sugar-cane cultivation on the black soil areas of the eastern tracts of the Central Provinces is the prevalence of red rot (*Colletotrichum falcatum* Went.), which, as is well-known, attacks the cane during the ripening period and leads to a great loss of sugar. This disease is also important in other parts of India, such as North Bihar, the Godavery delta in Madras, where soil-aeration difficulties are common. Some interesting results have been obtained by Clouston[1] in the Central Provinces on the effect of the physical texture of the soil on the resistance of the sugar-cane to this fungus. On the stiff black soils, in this track, red rot is common; on the neighbouring open porous *bhata* soils, however, crops as high as 40 tons of stripped cane to the acre are grown and there is a remarkable absence of the red rot fungus. There appears to be here a case well worthy of more detailed investigation. Soil-aeration and healthy root-development confer a high degree of immunity on the sugar-cane, while the poor physical texture of the black soils appears to render this crop exceedingly susceptible to red rot. The sugar-cane readily lends itself to the investigation of its root-system and of its juices, as the plant is large and abundant material for research is readily available at many centres.

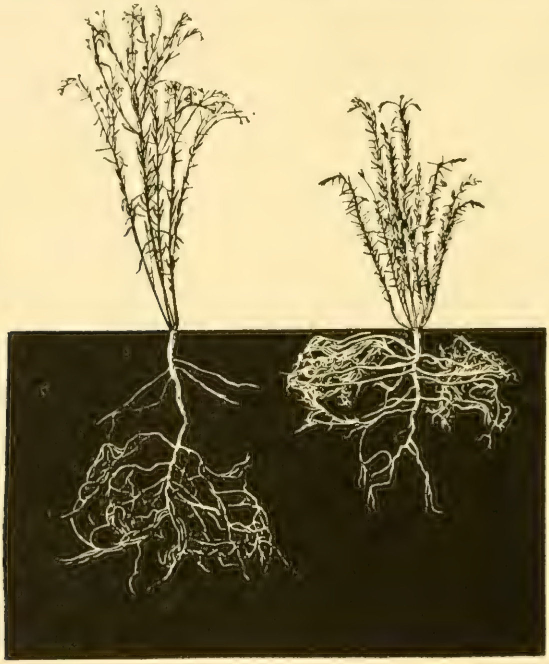

Fig. 5. Linseed from Central India (left) and the Indo-Gangetic alluvium (right).

The protection of fruit trees from green-fly. The usual method of controlling attacks of green-fly is to spray the trees with some wash in which soft soap is one of the chief constituents. In practice, however, this procedure is of limited value as the affected trees soon become re-infected and the process has to be repeated, an important matter now that labour is becoming so expensive. It is generally considered that the only cause of green-fly attacks is the insect itself. If this is so, there seems no reason why the pest should not spread rapidly in any garden after its first appearance in the spring. This was not the case in the Quetta fruit experiment station, where this pest has been under observation for some years. Frequently trees remained quite free from green-fly in the immediate neighbourhood of others badly affected, and this has happened year after year. It would appear, therefore, that something else besides the green-fly is necessary for successful infection to take place.

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[1] *Agr. Journ. of India,* Special Indian Science Congress Number, 1918, p. 89.

Some light has been thrown on the conditions necessary for green-fly attacks as the result of a number of irrigation experiments at Quetta. Following American experience on certain soils, an attempt was made to store up water in the subsoil during the winter and spring for use during the subsequent hot weather, when water is very scarce. The experiments were successful as far as the saving of summer watering was concerned but the system had to be given up on account of the rapid increase in green-fly attacks which accompanied the winter irrigation. After the summer, only one watering is now given in October so as to ensure a sufficient supply of moisture in the soil to prevent the freezing of the roots by early frosts before the winter rains begin. The cessation of winter watering has at once been followed by the recovery of the trees from green-fly attack.

Among the experiments which have been conducted on this subject, the following may be quoted:

1. Four heavy winter irrigations were applied to three plots of peaches and one of nectarines during the winter of 1915–16. In all cases, the trees were very badly attacked by green-fly during April, 1916, and the attack was much more severe than in the neighbouring gardens. Further watering was then stopped and the soil round the trees was broken up down to the upper roots. In this way aeration was restored, and after about a month the new growth produced was free from *Aphides*. The trees then presented a remarkable appearance. The first-formed leaves on each twig showed extensive damage by *Aphides*, the late formed leaves on the same branch were normal and perfectly healthy.

2. The above four plots were treated in quite a different manner during the winter of 1916–17. After the summer, only one watering

was given—on Sept. 30th—and during the winter and spring no irrigation water at all was applied. As a result these plots were practically free from green-fly, the trees grew vigorously and the foliage showed all the characteristic appearances of healthy peach trees. These plots stood out in marked contrast to many of the trees to be seen in the Civil Station when in 1917 the ravages of green-fly were far above the average.

3. Three lines of almonds (a deep-rooted tree), and a plot composed largely of various stocks including plums, almonds and peaches, which were clean cultivated in 1916 and which were remarkably healthy and quite free from green-fly, were sown with shaftal (*Trifolium resupinatum*) right up to the stems in August and September, 1916. Several waterings were applied to these trees during the winter and spring. All the almonds, the seedling peaches, and some of the plum stocks became badly affected by green-fly soon after the leaves appeared at the end of March, 1917. By May, the attack was severe and practically all the young growth was affected. In this case, trees free from green-fly in 1916 lost in a single season all their immunity as a result of winter watering.

4. A number of almond and peach trees—grown under a system of furrow irrigation by which over-watering is almost impossible—were planted in the autumn of 1916 close to one of the lines of almonds which was over-watered during the winter. The object of this was to obtain another demonstration of the fact that insects like *Aphides* are unable to attack healthy plants. The over-watered trees were all affected by green-fly which in no case spread to the plants which had been watered by furrows and which had obtained an abundant supply of air for their roots.

These results, which have been repeated on several occasions at Quetta, suggest that the control of green-fly must be sought elsewhere than in the destruction of the insect. Soil-texture and soil-aeration in Baluchistan are markedly improved by a winter fallow and are known to suffer from over-watering during the cold season. This appears to affect the development of the roots of fruit trees in the spring by interfering with soil-aeration. A change in the sap seems to result after which the trees become attacked by green-fly. The connection between winter irrigation and green-fly has been obtained so frequently and is so definite that more detailed investigations of the soil, of the root-system and of the sap of the trees affected by green-fly is urgently called for. If, as appears possible, it is found that the insect can only attack trees in an abnormal condition, the prospects of the efficient control of this pest becomes much more hopeful.

III. SOIL-TEMPERATURE.

Although soil-temperature is such an important factor in the distribution of the crops of India, both as regards season and the areas in which they occur, nevertheless but little attention has been paid to this growth factor in considering the incidence of disease. In India, the higher limit of temperature most frequently affects growth and in studying the crops of cold countries like wheat, which can only just be grown in India, this is one of the factors which frequently deserves attention.

White ants and wheat seedlings. One of the difficulties in wheat cultivation in Bihar and the eastern districts of the United Provinces is to establish the crop. If sown a few days too early, the seed germinates but the seedlings are rapidly destroyed by *Termites*, whole fields disappearing in a few days. The trouble became of some importance a few years ago in Bihar as it interfered with the raising of seed of the new Pusa wheats on some of the private seed farms[1]. The disease was particularly serious in years when the rains ceased early and when the last monsoon showers of early October, known locally as the *Lathia*, were not received. In such seasons, the advent of the cold weather is always postponed and the cool westerly breezes which normally set in about the middle of October are delayed till nearly the end of the month. The sowing time for wheat in Bihar in years when there is a good *Lathia* is just after the middle of the month and no trouble with white ants need then be feared. When, however, these sowing rains fail, nearly all the fields are destroyed by *Termites*. More damage occurs on low-lying damp heavy soil than on the higher and dryer areas. Examination of the root-system during the attack shows extensive discolouration of the new primary roots and of the first internode. Only in rare cases is there any formation of the secondary system. Before tillering can take place, the first internode is devoured by the white ants and the plants wither. A possible explanation of the trouble appeared to be a high soil-temperature which subsequent investigation seemed to confirm. In several seasons when the late rains failed, a comparison was made between sowings on Oct. 15th and others twelve days later. In addition to the delay, the furrows in the second case were left open for two or three days so as to cool the soil by evaporation. The early sowings were in every case destroyed by *Termites*, while in the later ones the damage was negligible and normal root-development and growth took place.

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[1] *Agr. Journ. of India*, XI, p. 351.

The simplest explanation of these results appeared to be a fall in the soil-temperature during the second half of October. That such a fall actually does take place is proved by an examination of a set of soil-temperature determinations made by Leake at Pemberandah in Bihar in 1903–4. In the year in which Leake's readings were taken, the *Lathia* amounted to 3·4 inches of rain and the daily soil-temperature at 4 inches at 1–2 p.m., fell gradually from 29·5° C. on Oct. 16th to 22° C. at the end of the month. This disease of wheat seedlings, which is very common in north-east India, is of some general interest, as the *Termites*, although the apparent cause of the trouble, were in reality engaged in the consumption of a moribund set of seedlings which had been practically destroyed, apparently by a soil-temperature above the maximum for growth. Examination of the root-system in this case provided the clue which soon led to the discovery of the cause of the trouble and to the working out of a simple remedy, which has since been widely adopted on the indigo estates of this tract.

The rust-resistance of einkorn[1]. Einkorn (*Tritrium monococcum vulgare* Kche.) is well known to be exceedingly resistant to the attacks of black rust (*Puccinea graminis* Pers.). In 1907, a plot of this wheat was grown at Pusa when it was found to be immune to all the three species of rust which occur in north-east India. The plants however were still in the vegetative condition at harvest time and were allowed to grow during the hot weather to see if any ears would form. No change of this kind took place but early in May they were found to be severely attacked by black rust. Here a prolonged rise of temperature led to the complete loss of disease-resistance in a species considered to be immune to this fungus. Unfortunately, the root-system at the time of the attack was not examined, as the observations were made some years before any attention was paid to such matters at Pusa.

The various diseases referred to in this paper are considered to establish a case for the detailed investigation of the root-systems of plants, combined with a consideration of the chief soil factors, in connection with the study of disease. There seems to be no doubt that the conditions of the active roots profoundly affects the resistance of the plant to the attacks of parasites. What this actually means in the processes of metabolism is a matter for further investigation. The discolouration and damage to the absorbing areas of the root are not unlikely to lead to the entry of substances into the crude sap which may entirely alter its value to the plant. This in turn would influence the cell-sap throughout the shoot-system. How such alterations affect the struggle between the protoplasm, on the one hand, and the hyphae of an invading fungus on the other and why insects like *Aphides* thrive on the juices of a Quetta almond tree grown in soil consolidated by over-irrigation the previous winter and disregard it altogether under a different system of soil management are interesting problems for the vegetable pathologist eager to break new ground and to carry his science beyond the beaten track.

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[1] *Journ. of Agr. Science*, II, p. 278.

The examples quoted suggest another direction in which a knowledge of the root-system is desirable, namely, in the determination of the factors on which the disease-resistance of a unit species depends. A collection of unit species grown under any particular set of soil conditions generally exhibit among themselves marked differences in disease-resistance. At Pusa, it has been found in several crops that an investigation of the root-system throws a considerable amount of light on this point. Both in the rains and in the cold weather, deep-rooted varieties yield less and are more liable to disease than shallow-rooted types. Soil-aeration and its consequences will probably be found to be an important factor in this case. Many more examples of disease-resistance in other parts of the world must, however, be examined before we can say how far immunity depends on morphological root-fitness for the environment and how far it is inherent in the natural resistance of the protoplasm to the invasion of a parasite.

THE PLANT AS AN INDEX OF SMOKE POLLUTION.

By ARTHUR G. RUSTON, B.A., B.Sc. (London), D.Sc. (Leeds).

Lecturer in Farm Economics, The University, Leeds.

(With Plates XXIV and XXV.)

In an earlier communication[1] an account was given of investigations carried out as to the nature and extent of atmospheric pollution by coal smoke in and near an industrial town. These investigations were at first limited to the area within a three mile radius of the centre of Leeds. Later, subsidised by a Government Grant from the Development Fund, they were extended to cover a wider area.

The information thus obtained, as to the relative freedom or otherwise of the various districts from pollution by coal smoke has been exceedingly valuable in studying not only the effects of that pollution on plant life, but also the ways in which the plant itself may be used as an index of the amount of that pollution.

1. In the first place the *General Type of Vegetation* in the smoke-infested areas is instructive in drawing broad conclusions as to the amount of smoke pollution.

Certain plants have been found to be resistant, and others particularly susceptible to smoke damage; and the presence or absence of some of these "Test Plants" is certainly suggestive.

The evergreens, which have to withstand the winter smoke are specially susceptible. Many of these in a smoke-infested area are quickly killed; others first become deciduous, and then finally disappear. Among the evergreens, the privet is particularly interesting as can be seen from the notes summarised in the following table.

District	Annual deposit of soot in tons per sq. mile	Observations with regard to the privet
3 miles to the north of Leeds	29	Evergreen, and flowers
2 ,, ,, ,,	42	Evergreen, but does not flower
1 mile ,, ,,	114	Few leaves only retained through winter
Centre of the city	243	Leaves fall in January
Industrial Leeds	539	Leaves fall in November

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[1] Crowther and Ruston, *Journal of Agricultural Science*, vol. IV, Part 1.

In Park Square, near the centre of the city, the laurel, aucuba and rhododendron are deciduous; while in Hunslet, the heart of industrial Leeds, even the box becomes deciduous, and the laurel is killed off in about two years.

Of the evergreens, the most susceptible are the conifers. These trees are xerophytic; their natural habitat is in a pure atmosphere at a high altitude, where the winds are high and the barometric pressure low, and where consequently evaporation from the leaf surface will be great. The soil, however, will be shallow and the roots none too plentifully supplied with moisture; hence there will be a constant necessity to husband the water supply as far as possible. This end has been effected in the evolution of the plant by the development of small leaf surface, and sunk stomata. Both of these characteristics, while useful in the natural habitat of the conifers, prove their undoing in a smoke-infested area. Conifers planted in Hunslet I have seen killed off in less than three months. Twelve years ago, more than twenty conifers were planted in the grounds of the Leeds University, one mile north from the centre of the city. At the end of three years not one was alive. The only two localities in Leeds, in which conifers attain even a moderate growth, are Roundhay and Weetwood, which the earlier investigations showed to possess the least smoke-infested atmosphere.

It is doubtful if they would ever do well in any district, where the annual deposit of soot amounts to more than 50 tons per square mile.

Plants whose leaves are possessed of a crinkled hairy surface, thus easily catching the soot, and of a thin cuticle readily damaged by the acid rain, are also particularly sensitive to smoke pollution. On the other hand, those possessing a hard smooth leathery type of leaf with thick epidermis, like many of the alpines, pinks, carnations, auriculas, London pride, and iris, are particularly resistant.

Thus the primrose does badly in Hunslet, makes little or no growth, rarely flowers, and never lives through more than one winter; while the auricula is as hardy as possible, and not only lives but thrives, grows and spreads. One border five yards long, which last spring was a mass of bloom, is the result of five years' propagation from four small plants. The geranium can be grown in a smoke-infested area, but the calceolaria is always a failure.

Perhaps no plant of this type gives a better index of the amount of smoke pollution than the hollyhock. Six years ago, eight hollyhocks (all propagated from the same parent plant) were planted in tubs containing soil taken from the same field of the Experimental Farm of the University of Leeds and the Yorkshire Council for Agricultural Education. The tubs were then placed, two at each station, in four different parts of Leeds. At only one station, that furthest north, did they flower the first year. In the second year more than eight feet of growth was made at Adel three miles to the north, while in the industrial area of Hunslet one plant only survived, a wizened, flowerless specimen, nine inches high.

Plants which have to "lay up a store for another year" tell their own tale of smoke pollution. Heavily handicapped in their growth by the effects of these atmospheric impurities they have little chance of laying up reserves. This is noticed both in the case of the bulbous and seed-bearing plants. Radishes will grow in Hunslet, but they will run to leaf and will not form bulbs. Tulips, narcissi, daffodils, scillas and hyacinths can be grown there and they will flower *one* year, but if a second year's bloom is desired, the bulbs must be replaced. Wheat, oats and barley can be grown in Hunslet, and you will get plants, but the grain, as can be seen from Fig. 1, Pl. XXIV, will not be worth the harvesting. You may grow lettuces and cabbages in Hunslet, but you must not expect them to heart.

A casual glance at the hedgerows will give some guide as to the extent of smoke pollution in any particular area, for the hawthorn is one of the smoke-sensitive plants and one of the first to go under.

Notice the flora of the lawns and fields of any particular district. In a smoke-infested area, the leguminous plants, the clovers and vetches will be conspicuous mainly by their absence. The finer grasses, particularly the fescues, will be missing. Coarse growing grasses like bent, couch and Yorkshire fog will be in the ascendant, and acid loving plants like dock, sorrel and plantain will abound. If a lawn is required in the industrial area of Leeds it must be sown down each year.

In the Hunslet Parish churchyard, surrounded on all sides by huge chimneys belching out smoke, even bent and the hardy *Poa annua* have been killed, and the only sign of vegetation is to be found in a few straggling blades of twitch still struggling for existence. The garden of a large residential house left stranded close to the church is a pitiable sight. Its only flower is the iris which still blooms freely, its only shrub or tree is the elder; its only fruit or vegetable is the rhubarb, and its only grass is twitch.

Though, apparently the elder will grow anywhere, no matter how great the pollution from coal smoke, it can still give some indication as to the amount of that pollution. Though it will grow in the industrial area of Hunslet, it will not flower. Though it will flower in the residential area of Headingley, two miles from the centre of Leeds, it will not fruit. Apparently it will not flower in localities where the annual deposit of soot is more than 200 tons per square mile, nor will it fruit if the annual deposit is greater than 50 tons per square mile.

Evidently the "General Type of Vegetation" in any one particular district will give some information as to the amount of pollution by coal smoke within the area.

2. The *General Appearance of Individual Plants* is also worthy of attention.

No one coming into Leeds by the Great Northern Railway and looking out of the carriage window near Ardsley station could doubt the fact that he was entering a smoke-infested area; for here almost every tree and every hedge has been killed. In the woods of Middleton and Templenewsam, the trees are to a great extent an index of the smoke pollution from colliery, coke oven and brickworks. Here many of the trees, particularly the ash, oak, elm and beech have been absolutely killed, most of them dying from the top. The main drift of the smoke from the industrial area of Hunslet can be easily traced almost to Garforth by the line of dead and dying trees.

Signs of smoke damage to trees can be discerned quite early in the year, in the appearance of the young shoots and buds, many of which are killed off before opening.

The leaf perhaps is the safest index. Before May is out, many leaves in smoky districts are showing characteristic brown blotches. In the case of leaves possessing a thin epidermis like the lime and sycamore, the signs of smoke damage are seen as in the case of Figs. 2 and 3, Pl. XXIV, all over the leaf, wherever the acid rain drops. In the case of the ribes (Fig. 4, Pl. XXV), the leaves of which possess a harder cuticle and have a tendency to offer a convex surface, the damage is shown by a red rim all round the edge. In the case of leaves like those of the laurel and aucuba which possess a hard cuticle and have a tendency to hang downwards, the damage is shown first at the tip of the leaf.

Evidence as to the amount of smoke pollution can also be obtained by the appearance of trees in the autumn; the greater the pollution the earlier the "leaf fall." Ash trees in the purer parts of Leeds often retain their leaves six or eight weeks longer than those in the more contaminated districts. Thus last year in Hunslet with an annual solid deposit of 539 tons per square mile, all the ash trees which remained alive had shed their leaves before the 18th of September, while at Roundhay with an annual solid deposit of 26 tons per square mile and no measurable acid deposit, practically all were in full leaf up to the beginning of November.

Evidence of smoke pollution is available at any time in the stunted growth of trees and shrubs, particularly of evergreens. The following particulars with reference to the maximum growth of aucubas in different parts of Leeds are striking.

		Annual deposit in tons per sq. mile		
District	Position	Total solid deposit	Sulphur compounds expressed as SO_3	Maximum height of aucuba found in district
Weetwood Lane	3 miles to north	42	28	10 ft. 6 in.
Headingley ...	2 ,, ,,	78	33	7 ft. 2 in.
University ...	1 mile ,,	114	38	5 ft. 8 in.
Park Square ...	Centre of city	243	56	3 ft. 2 in.
Hunslet ...	Industrial area	539	96	2 ft. 0 in.

Differences of the same order have been found in the case of the rhododendron and laurel.

Even the colour of the flowers in the gardens and woods will give some indication of the amount of smoke pollution. As a general rule the greater the pollution the paler the tint, and the more blues and reds will tend to run to white, and the bronzes to yellow. Intensely coloured flowers will show patches, the scarlet of the geranium in a smoke-infested district will be streaked with purple running to blue and even to white. The blood-red wallflower will be broadly streaked with yellow, and in a year or two most of the red will have disappeared.

Certainly the colour of the leaves will be more than suggestive, and signs of smoke pollution are to be found in the black deposit of soot and tar upon the leaf, and the absence of autumn tints.

3. Though, as has been seen, the "General Type of Vegetation" in a district and the "General Appearance of Individual Plants" will give much information as to the amount of smoke pollution in that district, most can be learnt by the "*Detailed Analysis*" *of the plant.* We may notice in a general way that the leaves of plants grown in the town are dirty. This can be readily seen from the photograph of the holly leaf grown in industrial Leeds (Fig. 5, Pl. XXV) and kindly placed at my disposal by Professor Cohen. The upper part of the leaf in question had first been cleaned, before dipping it in boiling water and extracting the chlorophyll with alcohol. We can, however, get a better idea of their relative cleanness or otherwise, by actually estimating the amount of solid deposit upon a unit area of these leaves. This has been done in

the case of a large variety of leaves, and the deposit thus found can easily be correlated with the known amount of smoke pollution in the district in which they have been grown.

The figures given are those found in the case of laurel leaves grown in the districts indicated.

District	Annual deposit of soot in tons per sq. mile	Deposit on leaf expressed in mgms. per sq. metre of leaf
Sutton	In the country free from smoke pollution	0
Weetwood Lane	42	158
University	114	718
Hunslet	539	1620

A microscopic examination of the leaf will reveal the fact that when the plants have been grown in a smoke-polluted atmosphere more or less of the stomatal openings will be choked with a tarry deposit. This will be particularly noticeable in the case of evergreens and most especially in the case of the conifers (Fig. 6, Pl. XXV). The leaves from a juniper grown at Garforth, six miles from Leeds, but well in the drift of the smoke from Hunslet, were examined by Mr Hector, Lecturer in Agricultural Botany, and he reported that 75 per cent. of the stomatal openings were more or less choked in this way.

We may notice in a general way that flowers grown in a smoke-polluted atmosphere lose their brightness of tint; but it is possible by means of a tintometer to get an accurate measure of their colour. I am indebted to Mr Frank of the Dyeing Department of the University of Leeds for the trouble he has taken in analysing by means of Lovibond's tintometer the colours of a large number of flowers. These flowers have been grown in each case from plants propagated at the Stapleton Gardens, Pontefract, from the same parent plant, by Mr Dobson, an old student of the Agricultural Department of the Leeds University, whose assistance in this and many other respects has been invaluable.

Three sets of readings are given.

Blood-red Wallflowers, June 13th, 1914.

		Direct tintometer readings			
District	Annual deposit	Red	Blue	Yellow	Total colour units
Weetwood Lane	42	36·5	7·0	4	47·5
University	114	22·5	2·5	9	34·0
Hunslet	539	13·0	1·1	9	23·1

Pyrethrum, June 28th, 1914.

		Direct tintometer readings			
District	Annual deposit	Red	Blue	Yellow	Total colour units
Weetwood Lane	42	38·6	3·8	0	42·4
University	114	30·0	2·8	0	32·8
Hunslet	539	26·0	1·5	0	27·5

Lupins, June 18th, 1918.

		Direct tintometer readings			
District	Growth	Red	Blue	Yellow	Total colour readings
Hunslet	1 year	10·0	10·2	0	20·2
,,	2 years	7·6	5·0	0	12·6
,,	3 years	4·4	3·2	0	7·6

The first one shows the tendency of all bronze flowers in a smoke-infested district to run to yellow: the second shows the cutting down of the red and blue tints and the third illustrates the fact that the longer a plant remains in a smoky atmosphere the more it loses the power of producing colour; evidently it is not simply a case of mere bleaching, but a radical change in the constitution of the plant.

We may notice casually the fact that smoke pollution means stunted growth, but we may get a measure both in the laboratory and *in situ* of the growth of plants, where the conditions other than atmospheric conditions are the same; and the relative growth will be found to be roughly inversely proportional to the smoke pollution. In the laboratory the relative growth has been measured by estimating the amount of carbon dioxide assimilated by a unit area of leaf in a unit of time. The following results refer to experiments made with laurel leaves of the current year's growth taken from shrubs grown in the districts mentioned.

	Annual deposit in tons per sq. mile	Relative assimilation of CO_2 per unit area of leaf in unit of time
Weetwood Lane	42	100
Headingley	78	53
Clarendon Road	200	15
Park Square	243	12

In situ the relative growth of plants in different districts has been compared, by filling large wooden buckets with soil taken from the same field in the country, sinking the buckets in gardens in different parts of the town, where the amount of smoke pollution has previously been determined; using the soil for growing a succession of crops each successive year and carefully weighing the produce. In selecting the various stations care was taken that the altitude, exposure and all other conditions other than atmospheric smoke pollution should be as nearly as possible identical. Apart from a few slight irregularities the results indicate a fairly close correlation between the relative degree of purity of the atmosphere in the neighbourhood of the station, as determined from earlier observations, and the actual amount of plant growth obtainable.

Station	Relative purity of air, as measured by freedom from sulphur	Relative weight of crop			
		1st crop Radishes 1911	2nd crop Lettuce 1912	3rd crop Cabbage 1913	4th crop Wallflower 1914
Weetwood Lane	100	100	100	100	100
Headingley	70	90	86	122	32
University	55	60	74	89	6
Park Square	37	49	40	37	2
Hunslet	34	46	31	15	3

An examination of the roots of plants will give some indication of the amount of smoke pollution; plants grown in soil that has been for long exposed to such pollution being marked by an almost entire absence of root hairs and fibrous roots. The differences in the root development of the wallflowers grown in soil which had been exposed in the various districts four years were most marked. Oats and barley were the following year grown in the same districts in the native soils and the differences in root development were still more marked.

An examination of a felled tree will often give valuable information as to the purity of the atmosphere in which it was grown. The tree automatically keeps a record of its yearly growth, and the presence of any inhibiting factor will make itself known by the narrowing of the annual rings. This is well seen in the case of the section of the Scotch fir shown in Fig. 7, Pl. XXV, for which I am indebted to Mr D. W. Steuart. The tree in question was grown at Broxburn, near the Roman Camp Shale Works, which were opened 17 years before the tree was cut down. In consequence of the acid fumes and smoke-contaminated atmosphere, the diameter growth as measured by the annual ring was sharply checked when the tree was 12 years old, though under normal circumstances it would be fairly constant up to 30 years old and then fall steadily off. This sharply defined check in the growth of the tree, as recorded by itself, is coincident with the opening of the Shale Works in 1893.

A chemical analysis of the plant will give exceedingly useful information as to the amount of smoke pollution in the district in which it was grown. In this connection the following analyses of the deposits on aucuba leaves carried out by the Air Analysis Committee of the Field Naturalists' Society of Manchester in the winter of 1890–91 are of interest.

Deposit on Aucuba Leaves.

In milligrams per square metre of leaf surface.

Date	Locality	Description	Solid deposit	Sulphuric acid	Hydrochloric acid
1890					
Dec. 14	Alexandra Park	Surburban	131	7·2	9·1
,, 13	Owens College	,,	315	10·4	17·3
,, 16	Hulme	,,	420	26·0	—
,, 14	Harpurhey	,,	443	19·0	4·4
,, 14	Infirmary	Urban	728	27·5	19·4
,, 13	Albert Square	,,	833	24·2	21·7
1891					
Jan. 17	Peel Park	Surburban	374	18·0	—
,, 22	Queen's Park	,,	194	17·5	—

It will be seen that the central localities show the largest deposits of soot and acid; the sulphuric acid there forming from 6 to 9 per cent. and the hydrochloric acid from 5 to 7 per cent. of the total deposit.

But these impurities due to smoke pollution get not only *on* the leaf but *in* it. It has already been seen that the stomata of leaves may be choked by a tarry deposit. The leaf may also absorb sulphur dioxide from the atmosphere partly through its stomata and partly in the case of some leaves possessing a thin cuticle directly through the epidermis. Hence the sulphur content of leaves will give perhaps one of the best indications of the amount of smoke pollution.

A very large number of leaves from different districts have been analysed in this way, the figures quoted are those connected with the laurel leaves referred to on p. 394, which were collected on February 15th, 1913.

District	Annual deposit of soot in tons per sq. mile	Percentage of SO_3 in dry matter of leaf
Sutton	Free from smoke pollution	0·31
Weetwood Lane	42	0·66
University	114	1·28
Hunslet	539	1·98

If this method is used for a comparison of the relative freedom from pollution of different districts, two or three points must be borne in mind. The leaves must be taken from the same variety of trees or shrubs, for different types of leaves will absorb sulphur dioxide at different rates and hence possess different proportions of SO_3. They must also be collected at the same time for the sulphur content of leaves will increase with age. The total sulphur content expressed as SO_3 of sycamore leaves grown in Meanwood and analysed by Steuart was 0·48 per cent. in May and 0·75 in August.

The sulphur present in the plant will be partly protein and partly non-protein; and leaves grown in a smoke-infested area will not only contain a large amount of sulphur; but that sulphur will be present principally in non-protein forms, mainly sulphates. The following analyses of elder leaves collected in June, 1913, at the stations mentioned illustrate this point.

Station	Yearly deposit of SO_3 in tons per sq. mile	Percentage of SO_3 in dry matter			Ratio		
		Protein	Non-protein	Total	Protein		Non-protein
Sutton	about 8	·21	·07	·28	300	:	100
Weetwood Lane	28	·20	·13	·33	154	:	100
Woodhouse Moor	38	·19	·18	·37	105	:	100
Hunslet	96	·11	·48	·59	23	:	100

In the autumn of 1919 the Department of Agriculture of this University was asked to investigate a bad case of smoke damage to a growing crop of four acres of potatoes. My estimate of the cost of growing and harvesting the crop, drawn up from the details of cultivation supplied by the owner was £98. 18*s*. In return for this outlay of nearly £100, two tons of marketable ware were lifted and sold for £18. 18*s*.; and approximately a ton and a half of small potatoes were fed to the pigs. This would mean that the actual loss in out-of-pocket expenses incurred by the grower could not possibly be less than £70 and most probably would be nearer £80. The haulms of the potatoes all showed marked signs of smoke damage, even to the eye. A chemical examination of these showed them to possess an abnormally high sulphur content, and a very low ratio of protein to non-protein sulphur. The total percentage of SO_3 present in the dry matter of the leaves was as high as 0·72 per cent., of which only 0·21 per cent. represented protein sulphur, and 0·51 per cent. represented non-protein sulphur.

A chemical analysis of plants grown in smoke-infested areas will also show that they contain proportions of arsenic increasing with the amount of the smoke pollution.

A *Bacteriological* examination of soils in smoke-polluted districts will also in many cases supply information which will be of service in determining the amount of that pollution. The acidity of the smoke will deplete the soil of its calcium carbonate and in so doing will modify to a large extent the number and activity of the soil flora. The greater the acidity of the soil the smaller the number of bacteria present in the soil, and the less their activity; the nitrifying organisms being found to be the most susceptible.

The following table gives the results of bacteriological examination of the soil taken from Garforth and exposed for three years in the districts mentioned.

				Nitrifying organisms	Putrefactive organisms	Nitrogen fixing organisms
District	Annual deposit in tons of SO_3 per sq. mile	Calcium carbonate in soil %	Total no. of bacteria per gram of dry soil Thousands	Ammonia converted into nitrates Mgms.	Ammonia produced from peptone Mgms.	Nitrogen fixed per gram of mannite Mgms.
Weetwood Lane	28	0·30	1536	8·7	105	26
Headingley	33	0·26	1236	6·4	88	21
University	38	0·19	1054	4·3	78	19
Park Square	56	0·17	876	1·9	67	18
Hunslet	96	0·12	798	1·2	64	15

These results indicate clearly that the detrimental effect of the smoky atmosphere upon plant growth is partly due to unfavourable changes in the soil—such as the steady depletion of the stock of calcium carbonate, and the inhibition of the activities of the nitrogen-adapting soil flora.

We may notice that plants grown in a smoke-polluted atmosphere lose their vitality; but it is possible in a large number of ways to get a measure of that loss of vitality and to use the information thus obtained to gauge the amount of smoke pollution in different districts.

This loss of vitality will be shown in a diminution of the *Reproductive Powers of the Plant*, whether propagated from seed or from cuttings.

(*a*) The following table gives the germination capacity of oats grown in 1913 at the stations indicated.

Station	Annual deposit in tons per sq. mile	Germination capacity (10 days)
Adel	29	98 %
Headingley	78	92
University	114	64
Hunslet	539	17

(*b*) 100 viola cuttings taken from plants grown in Roundhay (annual deposit 26 tons per square mile) were struck in Hunslet, and 98 per cent. grew.

100 viola cuttings taken from plants *grown* in Hunslet were struck in Hunslet, but not a single cutting grew.

It is shown in the *smallness* and *lack of weight of seeds* of plants grown in a smoke-infested area.

Weight of 100 *corns of barley grown from same seed.*

Where grown	Annual deposit in tons per sq. mile	Weight of 100 corns
Easingwold	Free from smoke pollution	4·85 gms.
Adel	29	4·81
Headingley	78	4·35
University	114	2·27
Hunslet	539	1·16

It is shown not only in the diminution of the germination capacity, but also in the diminution of the *Germination Energy*.

It is shown in the inability of the plant to put up a fight against adverse conditions, as for example, the winter frosts. To test this point nine cabbage plants were planted out in the autumn of 1913 at the five stations mentioned.

Station	Annual deposit in tons per sq. mile	Observation
Weetwood Lane	42	8 out of 9 survived the winter
Headingley	78	2 out of 9 survived the winter
University	114	6 dead by Christmas. Frost in February killed rest
Park Square	243	All dead by middle of November
Hunslet	539	All dead before end of October

Where the total annual smoke deposit exceeds 100 tons per square mile, it is dangerous to adopt autumn planting either of wallflowers, cabbages or spinach. Where that deposit exceeds 200 tons per square mile it is absolutely fatal. More than 100 wallflowers were planted out in Hunslet in September and not one stood the winter. They can be grown in smoke-polluted districts but they must be planted out in the spring.

The loss of vitality is shown perhaps most noticeably in the inhibition of the activity of the various *enzymes* or ferments which assist in the chemical processes taking place in the plant. The figures given in the following table refer to laurel leaves collected in February, 1913; and illustrate the way in which the activity of the various enzymes are influenced by smoke pollution.

District	Annual deposit in tons per sq. mile	Oxidase activity	Catalase activity	Emulsin activity
Sutton	Free from smoke pollution	100	100	100
Weetwood Lane	42	64	47	85
University	114	24	37	51
Hunslet	539	0	34	35

The relative lipase activity in the oat grain grown in 1915 in the districts mentioned was measured by allowing the enzymes present in the grain to hydrolise an ethereal salt like ethyl butyrate or ethyl acetate and observing the amounts of acid liberated by titration against $N/10$ NaOH. The results show that the activity of this enzyme as well as that of the others previously mentioned is inhibited by smoke pollution.

Effect of Smoke Pollution on Activity of Lipase in Oat Grain.

District	Relative activity of lipase
Adel	100
Weetwood Lane	75
Headingley	66
University	54
Hunslet	42

In conclusion, I should like to express my indebtedness to Professor Crowther and Professor Cohen for invaluable help and guidance all through the investigations; to Mr Hector for assistance given in the microscopic examination of many of the leaves; to Mr Frank for help given in the measurements of the tints of the flowers; to Professor Priestley for guidance in the estimation of enzyme activities; and to all those gentlemen who have so kindly placed their gardens at my disposal for so many years.

EXPLANATION OF PLATES XXIV, XXV

Fig. 1. Oats from same sample of seed grown in different districts in and round Leeds, Adel, three miles to north of Leeds, Hunslet, Industrial Leeds.

Fig. 2. Sycamore.

Fig. 3. Lime.

Fig. 4. Ribes. Smoke-damaged leaves collected 29 May, 1914; from Woodhouse Moor, one mile to the north of Leeds.

Fig. 5. Holly leaf obtained from tree growing in industrial Leeds. (Upper half cleaned: lower half showing deposit of soot.)

Fig. 6. Leaves of Conifers, collected at Garforth, showing "sunk stomata" choked with tar.

Fig. 7. Section of Scotch fir, grown at Broxburn, showing damage done by fumes from Roman Camp Shale Works.

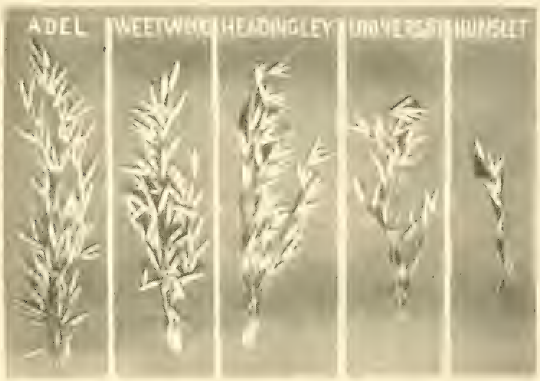

ADEL
WEETWOOD
HEADINGLEY
UNIVERSITY
HUNSLET

Fig. 1.

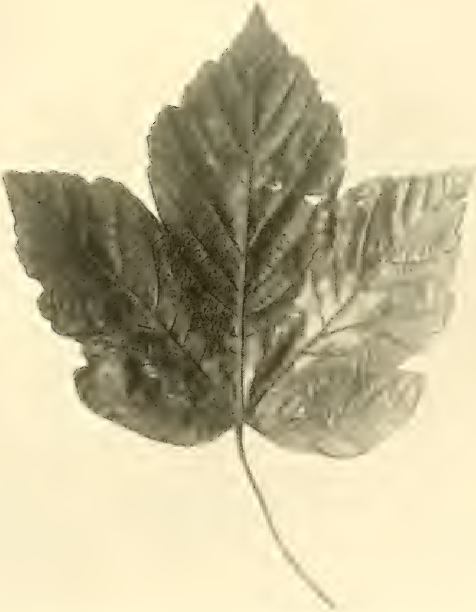


Fig. 2.

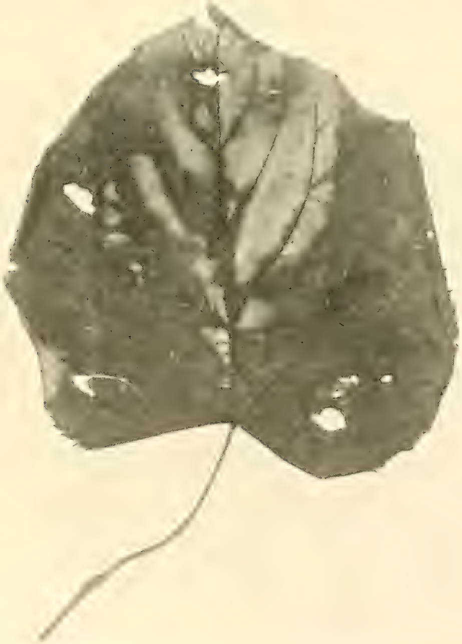


Fig. 3.

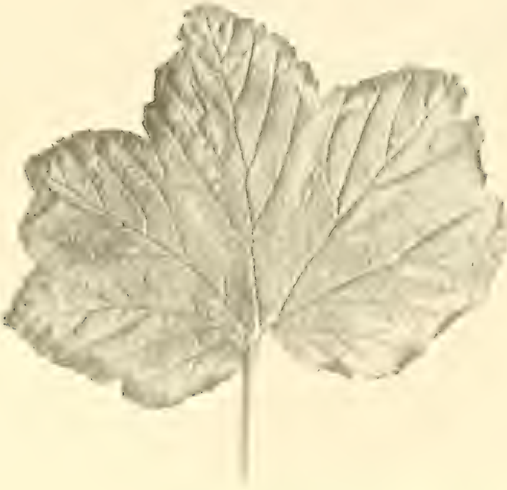
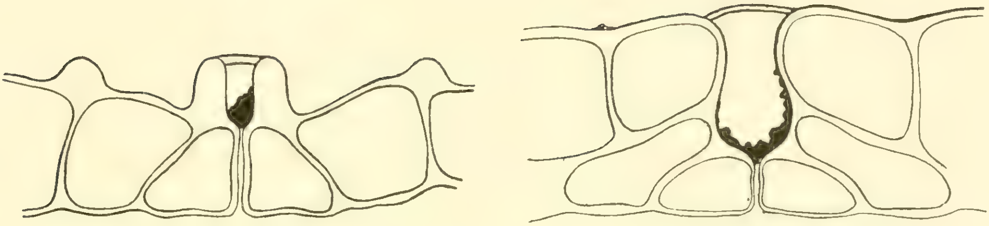


Fig. 4.



Stoma of juniper.

Stoma of silver fir.

Fig. 6.

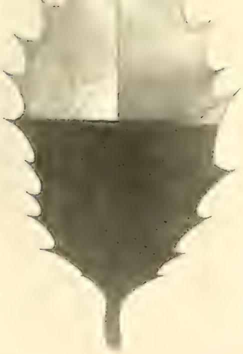


Fig. 5.

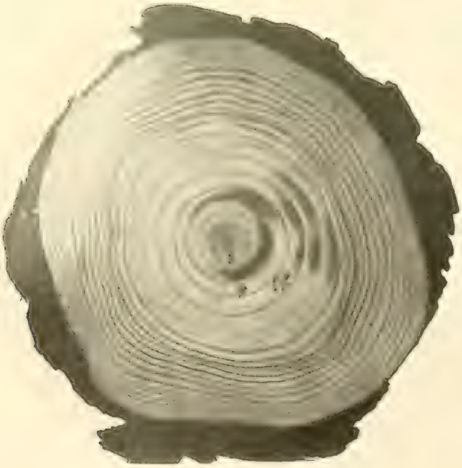


Fig. 7.

METHODS IN THE QUANTITATIVE ANALYSIS OF PLANT GROWTH—A REPLY TO CRITICISM.

BY G. E. BRIGGS, F. KIDD AND C. WEST.

THE Chief Statistician at the Rothamsted Experiment Station in his criticism of the methods put forward by us in recent articles(4 & 5) on The Quantitative Analysis of Plant Growth, summarises his remarks as follows. "The methods of calculation formulated by Briggs, Kidd and West for the analysis of plant growth are inaccurate." We feel that this sweeping statement standing in the forefront of the conclusions of what might appear to be an authoritative utterance by a statistician cannot be allowed to pass unanswered, the more so in that it is not supported by evidence or argument in the body of Mr Fisher's paper.

The Method.

The general method proposed by us for a quantitative analysis of plant growth is to obtain from primary data recorded at frequent intervals throughout the life of the plant, secondary relations[1]. We proposed the following as being probably the most useful at the outset.

1. Relative Growth Rate.
2. Leaf-Area Ratio.
3. Unit Leaf Rate.
4. Relative Leaf Growth Rate.

We suggested that by a careful comparison of these with each other and with records of environmental factors one might be able to disentangle problems of plant growth and thus eventually to evaluate plant constants. We do not wish it to be concluded that we proposed these as the only significant secondary relations. For example, from an analysis of the results of growth experiments carried out by us more recently it appears that the ratio of the rate of growth to the rate of respiration is a further significant secondary relation.

The question of the value of this general method is not dealt with by Mr Fisher, and indeed can only be decided by the results obtained from its application.

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[1] For details of these secondary relations the reader is referred to (5).

The Methods of calculating Secondary Data.

The question then arises, are the methods put forward by us for calculating the above secondary relations inaccurate? This seems to be the second possible interpretation of Mr Fisher's summary and is, moreover, what he literally states. In the first place, in spite of the conclusion quoted above, Mr Fisher deals only with the methods proposed for calculating Relative Growth Rate, R, and says nothing about the methods for calculating the other secondary data mentioned above. We defined R ((5), p. 204) as the weekly percentage rate at which the dry weight increases, and stated that if the rate were continuous compound interest the equation for calculating R would be

$$\frac{R}{100} = \log_e W_2 - \log_e W_1 \quad \text{......................(1)},$$

and if the rate were simple interest the equation would be

$$\frac{R}{100} = \frac{W_2 - W_1}{W_1} \quad \text{..........................(2)}.$$

Both these methods of calculation were put forward(5)[1]. Mr Fisher urges the use of the first, and states the second to be inaccurate. As a matter of fact both methods of calculation are perfectly in concordance with our definition and neither of them can be in itself characterised as inaccurate.

The Use of Relative Growth Rate Values.

A third possible explanation of Mr Fisher's criticism is that, instead of meaning the charge of inaccuracy to apply to our methods of calculation, he means it to apply to the use we have made of the values of the Relative Growth Rate calculated by means of equation (2). So far we have published a paper(4) in which the fact has been recorded that the Relative Growth Rate, calculated by *either* of the two methods described above, follows the generalised form of curve shown in Fig. 9 of the paper in question, and that the Leaf-Area Ratio curve follows a closely similar course. It was pointed out at the time that, for the purpose of demonstrating this fact, it is immaterial which of the two methods of calculation is utilised, and indeed, in Fig. 1 a comparison was made of the results obtained by the two methods. Mr Fisher has only elaborated this comparison. It was decided to present the majority of the results in that paper in the form adopted (*i.e.* calculated by equation (2)) in order that the calculation might be perfectly intelligible to non-mathematical readers. Mr Fisher's attack centres round this point and amounts to a statement that for statistical purposes the results obtained by equation (1) are preferable to those obtained by equation 2. Since we did not attempt any statistical correlations in the paper under consideration his criticism is irrelevant.

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[1] The definition of Relative Growth Rate given in (4, p. 105) is for the rate calculated on the simple interest basis. It must be understood that we do not suggest that the growth of a plant is a process of accumulation of dry-weight at either "continuous compound" or "simple" interest. On the one hand, the whole of the new material is not put out as new capital, and on the other hand there is an unknown time interval before any new material can become new capital.

Miss Brenchley, with Mr Fisher's help, has utilised Relative Growth Rates calculated by equation 1 for determining the correlation between growth rate and temperature and sunshine respectively (3). We agree that the values calculated from our first formula (equation 1) are the values to be utilised for statistical correlations provided due consideration be given to the complexity of the problem. We propose to consider this question in detail in another place.

The explanation of Mr Fisher's misunderstanding is most probably to be traced to the discrepancy between our definition of Relative Growth Rate and Mr Fisher's and to the fact that he imputes his definition to us. While we define the Relative Growth Rate as the weekly percentage rate at which the dry-weight increases, in a previous number of this *Journal* ((4), p. 104) we pointed out, as Mr Fisher himself quotes, that "the principle of the proposed method of expressing rate of growth is analogous to that of the method by which the rate of most reactions, both chemical and physiological, are expressed, namely, amount of change per unit of material per unit of time." This precise physico-chemical definition, to which we say our definition is only analogous, Mr Fisher adopts as a definition of Relative Growth Rate and imagines we have done likewise, which we have not. Our attitude is that until we gain a more thorough knowledge of the complexity of the processes involved in plant growth, the adoption of a definite physico-chemical conception is not warranted since it may lead to the mistaken impression that its adoption constitutes in itself an advance in physiological knowledge.

His charges of "inconsequent arbitrariness in method of calculation when contrasted with precision of definition," and his imputation that our choice of method of calculation is explainable by "the mistaken impression that the use of the logarithmic formula involves the assumption that the relative rate of increase is independent of time," when viewed in the light of the above discrepancy of definition can be readily explained.

With regard to the second paragraph of Mr Fisher's summary we do not wish to reopen the discussion on the significance of the "Efficiency Index." Equation (1) given above for calculating relative growth rates is the same as Blackman's formula for calculating the "Efficiency Index (1)." There is nothing original in the formula itself, but whereas we propose an analysis by an evaluation of the Relative Growth Rate for weekly or for shorter periods[1] throughout the life-cycle, Blackman (1) and Brenchley (2) used this formula indiscriminately for periods of widely varying length and covering widely different portions of the life-cycle.

BOTANY SCHOOL,
CAMBRIDGE.

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[1] We have used weekly periods as no data for shorter periods are at present available. Daily or half-daily measurements would provide data for a much deeper analysis.

A TOMATO CANKER.

By ETHEL M. DOIDGE,

(Assistant Chief and Senior Research Officer,
Division of Botany, Pretoria.)

(With 5 Text-figures and Plate XXVI.)

INTRODUCTION.

A DISEASE which may be described as a canker of tomatoes was first noticed in fruit on the Pretoria market during the summer of 1914. It is most prevalent from January to March, and during that period each year (1914-20) a large percentage of the fruit offered for sale was disfigured. Affected fruit rapidly becomes attacked by soft rot organisms which enter the fruit through cracks caused by the scab lesions and destroy it within a few days.

The incidence of the disease has a direct relation to the rainfall. Tomatoes which ripen in the early summer are seldom attacked, being grown under irrigation, and the disease is seldom observed up to the end of November. From November to January the temperature is high, and there is usually a considerable amount of rain; moist, humid conditions are favourable to the development of the disease. The fruit can only become seriously scabbed when it is attacked by the organism in the early stages of its development; this would account for the non-appearance of the disease before December or January. A few lesions are to be found on fruits as late as June, but the disease can be regarded as serious only during the summer months.

The occurrence of canker in fruit on the Pretoria market was suggestive of the fact that the disease occurred in market gardens in the district; several tomato growers were visited and the surmise found to be correct. Canker is a very common trouble in market and private gardens in the Pretoria district; it is reported to occur also in the Rustenburg district, but I have seen no specimens from there, and beyond this nothing is known of the distribution of the disease. It is not regarded as being of a very serious nature, but a large percentage of the fruit is disfigured, and much of it decays if it is kept for a few days after ripening. The summer of 1919–20, when most of the observations were made, was exceptionally dry: another season with heavier or more continuous rainfall the losses would probably be far more serious, and might ruin the whole crop.

The "canker" lesions differ from those caused by other tomato diseases attributed to bacteria. The wilt disease caused by *Bacterium solanacearum* Erw. Sm.(3) is a distinctly vascular trouble and causes a characteristic wilting of the plants. *Aplanobacter michiganense* is also found in the vessels(2). "Streak," described by Paine and Bewley as caused by *Bacillus Lathyri*, is characterised as the name suggests "by the formation of dark brown or black sunken patches on the stem," varying from small spots to long furrows or blazes(1)." On the fruit it forms light or dark brown sunken patches with round or irregular outline.

The effects of the canker organism on leaf, stem and fruit are widely different from any of these as will be evident from the detailed descriptions to be given later.

SYMPTOMS OF DISEASE.

On the leaves the first indication of infection is the appearance of numerous dark green, semi-translucent, water-soaked points on the under surface. In cases of artificial infection in autumn weather this occurred seven to eight days after inoculation, under summer conditions the progress of the disease may be more rapid. The spots increase in size and become round or irregular and about 2 mm. in diameter; they are slightly sunken and are often present in such numbers in the neighbourhood of the lateral veins and leaf margins, that they coalesce, and produce irregular, discoloured streaks. The colour soon changes from dark green to deep quaker drab[1] (Ridgway 51) or vinaceous slate (50). The discolouration penetrates to the upper surface, and the spots eventually consist of a smoke grey centre, which is then membranous and semi-translucent surrounded by a deep brownish drab margin.

Where the spots are numerous the intervening leaf tissue becomes dry, brown and brittle, the original lesions being still plainly visible in the dead areas. In this way the affected portions of the leaf, especially the edges and the tips, become dead and dry and break away, giving the leaves a very ragged appearance, and many of the smaller leaflets are altogether destroyed. Affected leaves show a tendency to curl inwards, and are more or less twisted and distorted.

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[1] The numbers quoted after name of colours refer to plates in Ridgway's *Colour Standards and Nomenclature.*

Spots on calyces, pedicels and young parts of the stem are similar in character to the leaf spots. On the calyx they may be numerous, but very minute and scattered, or less numerous and up to 2–3 mm. diameter, forming elongated streaks up to 5 or 6 mm. long.

Cankers are produced on older parts of the stem, especially where the tissues have been somewhat injured by friction or otherwise. At first there appear irregular, dark green water-soaked areas, which later become corky-looking, slightly raised, roughened and with numerous small longitudinal cracks. They are nearest tawny olive in colour. The surface has the appearance of having become blistered or raised by abnormal tissue development underneath, with subsequent cracking of the blistered areas. Cankers of irregular form and 1–2 cm. in diameter are not uncommon. The discoloration does not penetrate into the wood; it is apparently confined to the cortex and is quite superficial.

In the field, infected fruits are usually found immediately below diseased leaves and are doubtless infected during rainy weather by raindrops which fall on infected leaves and subsequently drip on to the young fruit. The majority of the fruit spots are at the stalk end, but they are also found scattered over the sides and, less frequently, on the blossom end.

A very minute green or brownish blister is the first indication of infection: this blister may remain minute, about 1 mm. diameter, or may increase in size up to about 3 mm. and become considerably raised above the normal fruit tissue. Occasionally, presumably when weather conditions are unfavourable, infection does not proceed further, and when the fruit is ripe these minute blister-like spots have almost the appearance of fly-specks (Plate XXVI, fig. 2).

In the large majority of cases the point of infection becomes surrounded by a dark green, water-soaked area which spreads considerably and then begins to discolour from the centre. The centre becomes deep slaty brown, merging into wood brown at the edges; a water-soaked margin about 1 mm. wide is still apparent whilst the organism is active. Finally the epidermis ruptures in the centre, showing whitish brown over the discoloured tissues like the broken edges of a blister. The spots are hard and scabby in texture and usually slightly convex, although in mature fruit they may lie in slight depressions owing to arrested growth at the point of infection (Plate XXVI, fig. 1).

Single scabs are usually not more than 5 mm. diameter, but they are often so numerous and close together that they coalesce, forming large, scabby areas several centimetres in extent. As the fruit ripens the tissues round the infected areas remains green, forming a green rim round the scabs which is conspicuous on the red fruit. The rifts in the epidermis become extended in cases of severe infection and whitish brown cracks are formed, many of them over 1 cm. in length and extending into unaffected tissue. These open the way for putrefactive organisms and the fruit usually rots within a few days after ripening. Thus the disease not only disfigures the fruit and reduces its market value, but seriously affects its keeping qualities.

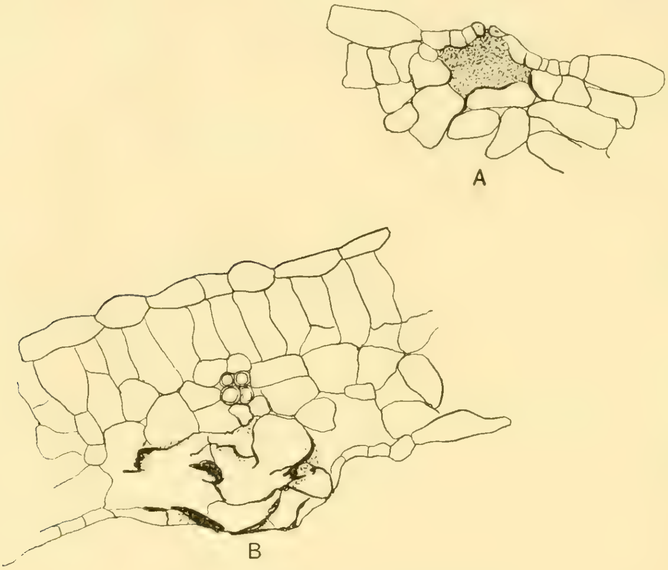

Fig. 1. Early stages in leaf infection.

Morbid Anatomy.

In inoculation experiments tomato leaves and fruit readily became infected without wounding, so that in all probability infection usually takes place through the stomata. This was confirmed by an examination of a large number of sections of spotted leaves: in the earliest stages of infection the bacteria are to be found in the sub-stomatal cavity (Fig. 1 A), and later make their way to the adjoining intercellular spaces. The middle lamella of the cells becomes much swollen, and stains an intense red in sections treated with carbol fuchsin and light green, the cells in the surrounding healthy tissue staining green (Fig. 1 B). As described by

Paine in connection with the "streak disease(1)," the cells become torn asunder by shrinkage of dead cells and by the tension set up by growth of the surrounding healthy tissue and eventually large cavities are produced. There are not many living bacteria to be found in the disorganised tissues, but at the edges of such lesions, where the organism is still active, large pockets of bacteria may be found. In the leaf the organism penetrates through the thickness of the leaf, entirely disorganising the tissue, but it does not travel far in a lateral direction. Stem lesions are very similar, but the organism has not been found to penetrate beyond the cortex.

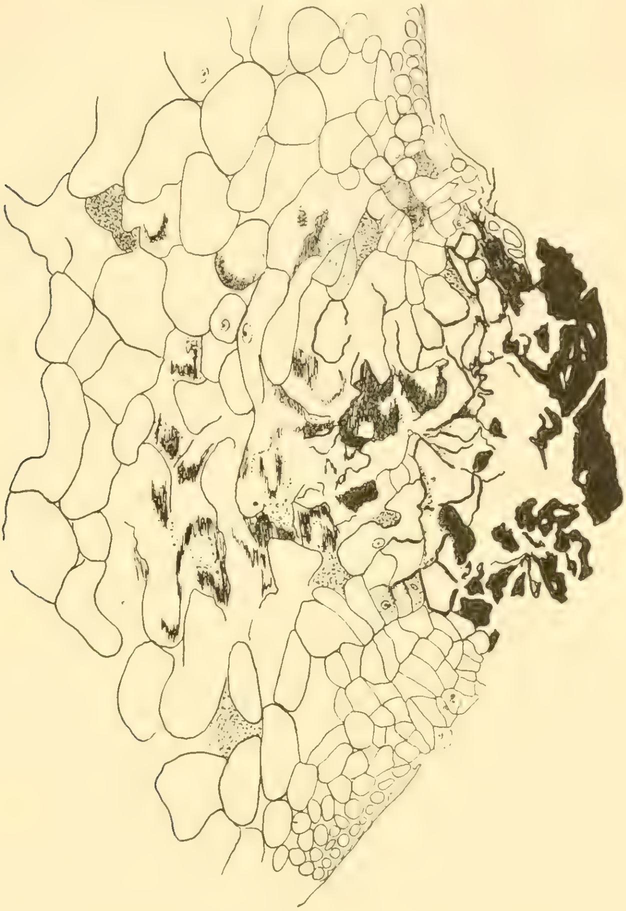

Fig. 2. Section through small lesion on fruit.

In the fruit a similar disorganisation of cells takes place, but the hypodermal cells at the edge of the injured tissue begin to divide actively (Fig. 2) and sometimes form a complete layer of new cells under the disorganised tissue (Fig. 3); this accounts for the convex contour of the canker. Sorauer (5) has illustrated a similar condition as a result of hail injury; it is probable therefore that the multiplication of cells is not due directly to the action of the organism but to the presence of dead tissue in the rapidly growing fruit.

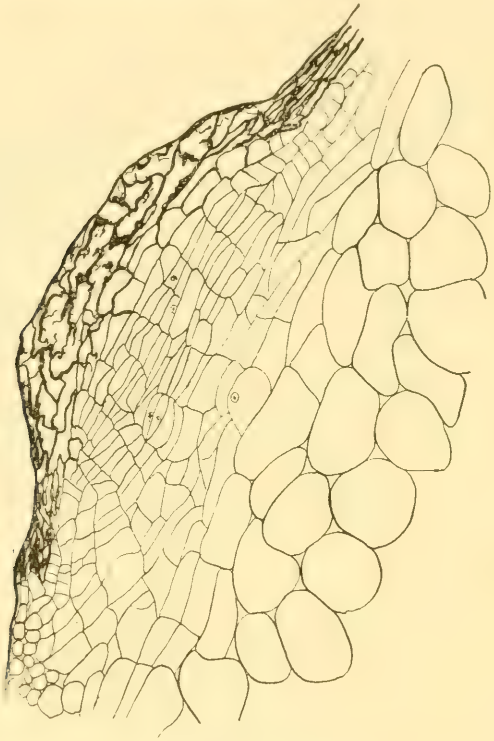

Fig. 3. Section through lesion on fruit, showing complete layer of actively dividing cells.

The nuclei in the affected cells become much hypertrophied, becoming five or six times the size of nuclei in healthy cells. The nucleolus becomes very large and vacuolate, and the nucleolar membrane disappears. There are frequently two nuclei in a cell or two nucleoli in one nucleus, the latter frequently irregular or lobed, being similar in shape to nuclei dividing amitotically as found by Smith (4) in crown gall lesions; but there was no clear evidence that the nuclei were dividing in this way.

In the entirely disorganised cells the nucleus continues to increase in size until the nuclear membrane is ruptured and the chromatin becomes diffused; the nucleolus remains intact for a considerable time, taking a red stain and standing out clearly in the disorganised mass.

ISOLATION OF THE CAUSAL ORGANISM.

The organism was first isolated in January, 1914, from tomatoes purchased on the Pretoria market. On these plates a yellow organism was predominant, but there were also colonies of a spreading, cream-coloured organism. At that time no greenhouse accommodation was available, and attempts to inoculate tomato plants out of doors during a spell of dry weather were unsuccessful; it was quite impossible to keep the atmosphere sufficiently moist. Attempts to inoculate detached fruits in the laboratory also proved a failure.

The disease was noticed on fruit exposed for sale each summer, but there was no further opportunity to investigate the matter until February, 1920. The organism was again plated out from fruit exposed for sale on the Pretoria market; colonies were visible after 48 hours, at 30° C., and in three days assumed their characteristic form and yellow colour. An almost pure culture was obtained direct from the host. The colonies were very similar in appearance to those of *Bacterium citri*, *B. campestre* and other related organisms; there appears to be a large number of plant parasites belonging to this group.

During March, 1920, the organism was repeatedly isolated from scabby fruit and infected leaves collected in a market garden at Daspoort, near Pretoria. In each case a pure culture of the organism was obtained without difficulty, from both leaf and fruit. It is more easily isolated from the fruit since the surface can be sterilised and the culture made from the tissue underneath.

INOCULATION EXPERIMENTS.

Preliminary Experiments.

A.

28. 1. 20. Two well-grown tomato plants were used bearing green fruit, almost full grown. The fruits were inoculated with a culture isolated from tomato fruits purchased on the Pretoria market. The culture was applied with a camel's hair brush, a few tomatoes on each plant being pricked and the rest uninjured. Inoculated fruit was covered for 24 hours with beakers covered with brown paper and plugged with cotton wool.

12. 2. 20. Dark green, water-soaked areas round needle pricks.

16. 2. 20. Two tomatoes ripened and were removed from plant; tissue round needle prick has remained green with a slight tendency to brown discolouration and are crowded with bacteria.

25. 2. 20. Remaining fruit ripened and picked. All calyces show numerous infections, but fruit infections have not gone beyond the green, water-soaked stage. Stems show extensive cankers where they were slightly injured by friction of beaker placed over fruits after inoculation. Control plants remained sound and showed no sign of infection.

B.

10. 3. 20. Three large tomato plants were used, bearing fruit at various stages of development. Some fruits were left uninjured, others pricked or lightly scratched. The culture was applied to fruits and leafy tips with a camel's hair brush, and the plants atomised with water. The leaves were left uninjured. All inoculated portions were covered for 24 hours with butter paper bags, to prevent excessive drying.

13. 3. 20. Numerous minute light and dark brown specks on younger fruits.

18. 3. 20. Numerous minute, water-soaked spots on leaves, also indications of infection round needle pricks on fruit.

23. 3. 20. Tomatoes which were very young when inoculated and which were not pricked show minute brownish blisters all over the surface. One which had only just set when inoculated had an irregular water-soaked zone round the blisters up to 2 mm. diameter. Leaf infections increasing in size and number and assuming characteristic purplish grey colour. Infected spots also visible on calyces, pedicels and stems.

29. 3. 20. Spots on small tomato mentioned above beginning to discolour: water-soaked zone round blisters on slightly larger fruit and round needle pricks on fruit which was inoculated by puncture when almost full grown.

12. 4. 20. Scabs on all fruits now quite typical; they have discoloured, become brown, epidermis has blistered and cracked in several directions. Badly infected leaflets become entirely yellow and dead.

13. 4. 20. Plants discarded. Control plants showed no sign of infection.

C.

29. 3. 20. Eight young plants about 1 ft. high were used. They were inoculated by atomising with culture isolated from artificially infected plant described in experiment B.

6. 4. 20. Numerous minute, water-soaked areas observed on younger leaves.

13. 4. 20. Leaf spots have assumed typical form and colour. Control plants showed no sign of infection.

D.

10. 5. 20. One tomato plant in bearing was inoculated. Fruits of various sizes and leafy tips were inoculated without wounding, and covered with butter paper bags for 24 hours.

19. 5. 20. Small raised spots visible on fruits, water-soaked spots on leaves. (The majority of the affected fruits and leaves were removed for purpose of studying morbid anatomy.)

Cross Inoculations.

It has been mentioned that the organism belongs to what Smith once termed the "yellow *Pseudomonas* group." Since five other organisms of this group were under observation at the time, and all are very similar in culture, it was thought advisable to carry out a series of cross inoculations. All these organisms infect their hosts by way of stomata or water pores; the inoculations were therefore made without wounding the plants.

A.

24. 3. 20. Six tins (1–6), each containing four young tomato plants, were used. These plants were about 1 ft. high and growing vigorously. One set of four plants (1) was inoculated with a culture of *Bacterium campestre*, one (2) with *B. citri*, and one each with (3) *B. Juglandis*, (4) *B. Phaseoli*, (5) *B. malvacearum*, and (6) the tomato organism.

31. 3. 20. Numerous minute, water-soaked spots on tomato seedlings inoculated with organism (6) from tomato scab. Other plants show no infection.

6. 4. 20. Spots on tomato seedlings in tin (6) have now assumed characteristic form and colour. All plants in tins (1–5) perfectly sound and showing no signs of infection.

13. 4. 20. No further development.

B.

24. 3. 20. Six tins of lemon seedlings were used, each containing six plants 10–15 inches high. One group of six seedlings was inoculated with each of the organisms mentioned in experiment A. The tins were numbered (1–6) as follows: (1) inoculated with *Bacterium campestre*, (2) with *B. citri*, (3) *B. Juglandis*, (4) *B. Phaseoli*, (5) *B. malvacearum*, (6) *Bacterium* causing tomato scab.

30. 3. 20. Incipient cankers noticed on lemon seedlings (2) inoculated with *B. citri*.

7. 4. 20. Cankers on seedlings (2) increasing in size and number. No sign of infection on plants inoculated with other organisms.

15. 4. 20. Numerous typical citrus canker lesions on leaves and stems in tin (2). All other plants have remained sound and show no sign of infection.

C.

24. 3. 20. Six cotton plants 2 ft. to 2 ft. 6 in. high were employed, one plant being inoculated with each of the six organisms mentioned in connection with experiments A and B.

29. 3. 20. Numerous minute, water-soaked spots on young leaves of plant (5) inoculated with *B. malvacearum*.

7. 4. 20. Spots have increased in size and assumed characteristic angular outline.

15. 4. 20. Leaf spots on plant (5) have discoloured, and are now dark brown or black. Cotton plants (1–4) and (6) inoculated with other organisms show no sign of infection.

D.

14. 4. 20. Six young walnut trees planted in separate tins were numbered (1–6) and inoculated with the six organisms tested in experiments A–C.

19. 4. 20. Numerous minute water-soaked spots on young leaves on tree (3) which was inoculated with *B. Juglandis.*

5. 5. 20. Spots on tree (3) have discoloured and assumed typical appearance of walnut blight lesions. All other trees remained sound and showed no sign of infection.

E.

14. 4. 20. Six tins each containing four well-grown cabbage seedlings were used; the tins were numbered (1–6), the four plants in each being inoculated with one of the same six organisms.

24. 4. 20. There is an indication of blackening of veins at edges of some of the leaves in tin (1), plants inoculated with *B. campestre.*

12. 5. 20. Cabbage plants in tin (1) show typical black rot lesions. No sign of infection in any of the other tins (2–6).

F.

14. 4. 20. Four bean seedlings were inoculated with each of the six organisms. Tins again numbered (1–6), four seedlings in each, and inoculated in the same sequence as in experiment A.

19. 4. 20. A few water-soaked areas visible on leaves of plants in tin (4) inoculated with *B. Phaseoli.*

20. 4. 20. Very numerous points of infection now visible on plants in tin (4).

30. 4. 20. Leaves of bean plants in tin (4) now heavily infected and showing numerous typical bean blight lesions. No sign of infection on plants in tins (1–3) and (5–6) inoculated with other organisms.

Inoculation on to other Hosts.

A.

7. 4. 20. 12 tobacco seedlings about six inches high were atomised with a culture of the tomato organism.

13. 4. 20. No sign of infection.

7. 5. 20. Still no sign of infection—plants discarded.

B.

7. 4. 20. Two plants of *Physalis minima* were inoculated by atomising with a suspension of a potato culture.

13. 4. 20. Numerous minute water-soaked spots observed on younger leaves.

17. 4. 20. Spots have increased in size, are somewhat angular, and are becoming brown. Control plants show no sign of infection. Re-isolated organism from infected leaves and found it to be identical with the original.

C.

7. 4. 20. One plant of *Datura stramonium* var. *tatula* was inoculated by atomising with a suspension of a culture of the tomato organism.

13. 4. 20. Numerous minute, water-soaked points on younger leaves: tissues on examination prove to be full of bacteria.

17. 4. 20. On *Datura* plant inoculated, organism has produced very numerous spots about 1 mm. diameter and somewhat angular, these are brown and membranous in centre and have a water-soaked margin: these brown spots show a tendency, especially in the younger leaves, to break away and cause a shot-hole effect. Control plant is healthy and shows a sign of infection; replated organism from infected leaves and found it identical with original.

D.

7. 4. 20. One plant of *Solanum incanum* inoculated without wounding.

17. 4. 20. No signs of infection on this or later date; leaf is protected by thick covering of hairs.

E.

7. 4. 20. One plant of *Solanum nigrum,* inoculated without wounding.

13. 4. 20. Slight indications of infection on younger leaves.

17. 4. 20. Infected spots have developed considerably, but are still small: they are irregular in outline, 1 mm. diameter or up to 2 mm. long, and are light brown and membranous in the centre. Replated organism and found it identical with original. Control plant showed no sign of infection.

F.

24. 7. 20. A number of sweet pea plants were inoculated by needle pricks in the stem. The result was entirely negative.

DESCRIPTION OF THE CAUSAL ORGANISM.

A. *Morphological Characters.*

When taken direct from the tissues of the host the organism is very variable in size and form: the majority are rather stout rods with rounded ends, but some are so short as to resemble coccus forms. They vary from ·6 to 4μ in length, and from ·5 to $\cdot75\mu$ in breadth. The majority are $1\text{–}1\cdot5 \times \cdot6\text{–}\cdot7\mu$.

In young agar cultures (24 hours at 30° C.) the organism is a rod with rounded ends, occurring singly or in pairs, or less frequently in short chains of three to seven elements. The rods are for the most part fairly even in size, measuring $1\text{–}1\cdot5 \times \cdot6\text{–}\cdot7\mu$; the extremes observed were $\cdot8\text{–}3\times\cdot6\text{–}\cdot7\mu$. In old cultures they are less regular, and short forms are numerous.

In young bouillon cultures the rods are similar in form. The organism grows rather reluctantly in neutral bouillon, and in six days old cultures in this medium there are numerous straight or curved rods 4 and 5μ long and also long undivided threads up to 50μ long.

On gelatine the average length is slightly greater, being 2–3 μ, and the breadth is ·6 to ·65 μ. Limits observed were 1–4 × ·6–·7 μ. The rods were mostly single but occasionally in pairs or short chains.

In 24 hours old potato cultures the rods are also rather long as compared with those on agar cultures; the majority are 1·5–2·5 × ·6 μ. There are numerous pairs and short chains, and occasionally long threads up to 40 μ long which are only partially or imperfectly segmented. After six days the size and grouping remain the same, with the exception of the long threads which are no longer seen.

Motility. The organism is actively motile in very young cultures. In hanging drop cultures it moves with a forward screwlike action, its progress being frequently interrupted by rotations on its short axis and other tumbling movements. The rods gradually made their way to the edge of the drop and came to rest. The organism is not motile as it diffuses from the tissues of the host. Rods from a young agar culture examined with the dark ground illumination showed no highly refractive granules, and the rods are apparently motile by means of a polar flagellum on the forward end which whirls like the propellor of an aeroplane.

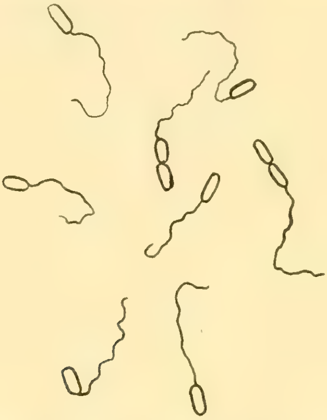

Fig. 4. Rods from streak incubated for 18 hours at 20° C.
Stained by Löffler's method.

This observation was confirmed by the examination of stained preparations. Good preparations were not very easy to obtain as the organism sheds its flagella very readily; fairly good results were obtained with a modification of Löffler's method and by van Ermengen's method. There is a single polar flagellum with a length of about 5–10 μ (Fig. 4).

Spores were not observed.

Capsules. The viscid nature of the growth on agar and other media points to the presence of a capsule. This is most clearly seen in potato cultures. Examined after 24 hours at 30° C. each rod is surrounded by a white halo; when stained with carbol fuchsin the rod stains intensely and the capsule is pale with a feebly stained margin (Fig. 5). As the culture grows older the capsule becomes more evident, and when stained with carbol fuchsin the rod and capsule stained as described above are embedded in a slimy mass which stains pink.

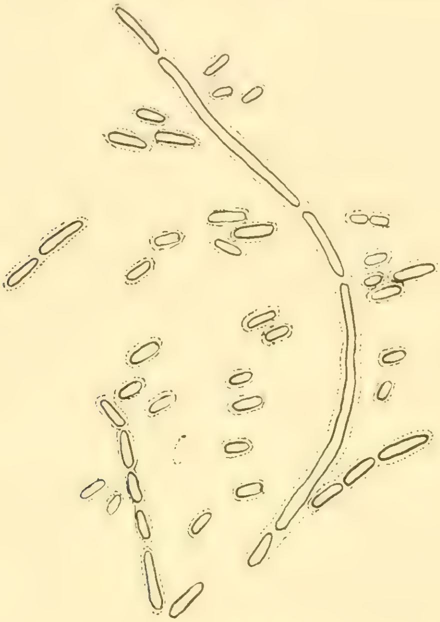

Fig. 5. Rods from potato culture, 24 hours at 30° C. Stained with carbol fuchsin.

Involution forms have been found in old gelatine cultures. They vary much in form; some are stout rods about 1 μ thick in the centre and tapering to pointed ends: others are longer threads up to 35 μ long and varying in thickness, curved and distorted and with or without constrictions at irregular intervals.

Staining reactions. The organism as taken from young cultures stains evenly and intensely with carbol fuchsin and all the ordinary aniline stains. In rods from older cultures all staining is fainter and more irregular. It is not acid fast and stains only faintly with Löffler's blue; it is Gram positive: no granules were observed in rods stained by Neisser's method.

Cultural Characters.

Preliminary cultivation was carried out as suggested by the Society of American Bacteriologists. In all cases, unless otherwise stated, cultures were incubated at 30° C.

Plate cultures on nutrient agar + 15. Colonies show as minute, shining points after 48 hours. By the third day they have increased somewhat in size, and are coppery, translucent by transmitted light, and yellowish or somewhat opalescent by reflected light. There is seldom any development after the fourth day; on thinly sown plates fully developed surface colonies are circular or oval, up to 5 mm. diameter, semi-translucent, colour Naples yellow (XVI). The margin is entire and texture homogeneous, finely granular as seen under the low power of the microscope. In some there is a faint indication of concentric zoning, but this is more evident in the bluish white colonies about 2 mm. in diameter, formed between the agar and the bottom of the plate. Long feathery crystals begin to form in the medium after about ten days. Submerged colonies are minute and lenticular, and often form surface colonies by excentric development.

Streak cultures on nutrient agar + 15. After 24 hours the streak is smooth, slightly convex, wet-shining, with entire margin, and about 5 mm. broad. The growth increases somewhat up to the third or fourth day, entirely covering the wetter part of the medium at the base of the tube. The colour is Naples yellow, and growth shows irregular, semi-opaque streaks when held up to the light. There is a heavy growth in the condensation water. Crystals begin to form under the streak at the end of the first week.

Stab cultures in nutrient agar + 15. Surface growth only; no growth in the depths of the medium.

Shake cultures in nutrient agar + 15. Numerous surface colonies develop and become confluent, entirely covering surface. There are some very minute submerged colonies just below the surface but none in the depths of the medium.

Plate cultures on nutrient gelatine + 15. All gelatine cultures were incubated at 20–22° C. Colonies were visible on the third day; on the fourth day thickly sown plates were partly liquefied, on more thinly sown plates surface colonies were up to 1 mm. diameter, convex glistening, cream colour, translucent, context homogeneous and finely granular; submerged colonies minute, opaque, lenticular. On the sixth day thickly sown plates were completely liquefied; in more thinly sown plates the colonies were up to 5 mm. diameter and each sunken in a saucer of liquefaction, the liquefied gelatine was clear and the colonies denser in the centre than at the circumference. On the tenth day the gelatine in the thinly sown plates was completely liquefied, the medium being very slightly clouded. Colonies were still intact but somewhat diffused, up to 15 mm. diameter and often rolled at the edges; they were not tough, but gelatinous in consistency, breaking very readily if an attempt were made to lift them with a needle. Under the low power of the microscope the centre was moruloid to grumose.

Stab cultures in nutrient gelatine +15. After 24 hours there were slight indications of growth at the surface and along the upper part of the stab, and on the third day there was a shallow crater of liquefaction at the surface. On the fourth day liquefaction was crateriform, 7-10 mm. wide and about 5 mm. deep; there was a good surface growth and a slight bacterial deposit on the unliquefied gelatine, but the liquefied part of the medium was colourless. Subsequently liquefaction became stratiform, and when it had proceeded to a depth of about 1½ cm. growth apparently ceased. The gelatine remained clear or very slightly cloudy, and eventually the surface growth sank to the bottom of the liquefied portion.

Streak cultures on nutrient gelatine +15. A whitish streak about 1 mm. wide is visible after 24 hours, which is replaced on the second day by a narrow channel of liquefaction along the needle track; this channel gradually becomes more extensive, the bacterial growth being carried with the liquefied gelatine to the bottom of the tube. This continues until there is 1–1·5 cm. of liquefied gelatine at the bottom of the tube.

Shake cultures in nutrient gelatine +15. Numerous minute surface colonies appeared in the third day, and the gelatine was slowly liquefied from the surface downwards, liquefaction being first noticed on the fourth day. At no time was there any growth in the depth of the medium.

Potato. On steamed potato cylinders a spreading, wet-shining butyrous growth covered the moister parts of the cylinder in 24 to 48 hours; on the sloping surface there was a broad, more or less raised streak surrounded by a narrow white "fermentation zone." The growth was amber yellow, and became somewhat viscid, especially in old cultures; it increased in quantity, covering the whole cylinder unless the medium was dry; the colour deepened somewhat with age and the medium was somewhat greyed.

Carrot. On steamed carrot the organism produces in three days a spreading, wet-shining, cream-coloured growth, practically covering the medium, and a thick shiny growth on the surface of the liquid at the bottom of the tube; the colour deepened after the first few days, becoming straw yellow to amber yellow.

Turnip. On steamed turnip cylinders growth is similar to that on carrot. The cylinder is entirely covered after three days with wet-shining, slimy-looking growth, which may be flat and smooth or somewhat raised, standing out on the surface in large drops. The colour is cream to straw yellow.

Parsnip. On steamed cylinders of parsnip, growth is similar to that on other vegetable cylinders described but rather less copious. The colour is straw yellow to amber yellow.

Beet. A very copious, spreading, wet-shining growth is also obtained on steamed cylinders of beet; the growth is more raised than on the other media and straw yellow in colour. On all steamed vegetable cylinders the amount of growth varies with the amount of moisture present, the best growth being obtained with the maximum amount of moisture.

Steamed rice. The rice grains become thinly covered with a spreading wet-shining growth which is straw yellow on the wetter parts of the medium and becomes light ochraceous buff where there is less moisture.

Sweet potato was a very favourable medium, growth being similar to that on the ordinary potato tubes.

Streak cultures on Loëffler's blood serum. Growth was fairly abundant, in the form of a wet-shining, cream-coloured streak along the needle track; liquefaction was observed on the sixth day and proceeded slowly.

Nutrient bouillon +15. Growth in bouillon varies considerably with the reaction of the medium. In tubes with a reaction of +15 of Fuller's scale the bouillon is faintly clouded after 48 hours; it never becomes turbid. A straw yellow ring 1–2 mm. broad forms above the liquid and there are often minute, whitish flocculent particles suspended in the liquid which eventually sink and form a sediment. In + 20 bouillon there is a slight pellicle formed, which sinks when disturbed, and considerable sediment is produced.

Durham's solution becomes lightly clouded. There is no ring, but often a few very minute flocculi in suspension which eventually sink and form a slight sediment.

Uschinsky's solution. There is no growth in this medium; it was kept under observation for 20 days.

Cohn's solution. No growth.

Egg albumen medium containing 1 gm. of powdered egg albumen and 50 c.c. of a ·05 per cent. solution of potassium phosphate became well clouded, but there was no ring or pellicle formation and no discolouration of the medium.

Fermi's solution becomes lightly clouded on the second day. Growth proceeds slowly and after about three weeks there is a good ring above the medium, and considerable sediment at the bottom of the tube. This is Naples yellow in colour and very viscid, rising in a spiral swirl when the tube is rotated.

Cabbage broth clouds fairly heavily: a ring forms above the medium and there is some indication of pellicle formation; there is also a sediment at the bottom of the tube.

Milk shows no change until the third day; separation of the whey takes place slowly in such a way that there is an increasing quantity of clear yellowish whey at the surface, and the lower part of the tube is filled with whitish minute flocculent particles. The clot is not coagulated, and is slowly digested, but had not completely disappeared in cultures which had been under observation for some weeks. The whey is clear and yellowish in colour.

In litmus milk the colour is partially reduced, and the culture becomes slightly more acid than the control. In flasks, where a greater part of the medium is exposed to the air the action of the bacterium is considerably more rapid than in tubes.

Physical and Biochemical Relations.

Proteolytic activity in milk. In describing the cultural characters of the organism, it has been stated that milk is slowly peptonised. A number of flasks each containing 50 c.c. of milk were tested at intervals of five days for peptone, tyrosine and tryptophane. At the end of five and ten days at 30° C. the culture fluid gave positive reactions for each of these compounds. In each case the reaction was stronger on the 15th and 20th day, particularly in the case of tyrosin for which an intense reaction was obtained on the 20th day. There was also a strong reaction for peptone on the 20th day.

A similar set of flasks was tested quantitatively for the production of amino-acids and ammonia. The following figures give the results from one such experiment.

Ammonia by distillation.

	Number of c.c $N/10$ acid neutralised			N as ammonia
	Culture	Control	– Control	approx. figure
5 days	4·27	3·40	·87	·0022 grm.
10 ,,	14·14	3·07	11·07	·0155 ,,
15 ,,	24·90	2·80	22·10	·0309 ,,
20 ,,	35·33	4·76	30·57	·0428 ,,

From these figures it will be seen that the amount of ammonia increases steadily up to the 20th day. Similar results were obtained from other tests carried out on the same lines.

The amount of amino-acids was estimated by the Sorensen method; it increases up to the 15th day and then decreases, the amino-acids being probably broken down to ammonia.

	Amount of $N/10$ NaOH used for final titration				N as
	Culture	Control	– Control	– Ammonia	amino-acids
5 days	9·57	8·33	1·24	·37	·00005 grm.
10 ,,	34·42	9·61	24·81	13·74	·0192 ,,
15 ,,	47·08	4·00	43·08	20·98	·0294 ,,
20 ,,	48·42	8·27	40·14	9·58	·0134 ,,

In *egg albumen* medium (1 gm. egg albumen in 50 c.c. of 0·5 per cent. potassium phosphate) similar results were obtained. The qualitative test showed that less tyrosin was formed than in the milk cultures, but a strong reaction for peptone was obtained all through.

The culture and control were tested for amino-acids and ammonia in the same way as the milk flasks. To an additional flask, zinc sulphate was added to complete saturation, and the total nitrogen in the filtrate determined by the Kjeldahl process; this gave nitrogen as peptone plus amino-acids and ammonia, and by subtraction nitrogen as peptone. It will not be necessary to give detailed figures as in the previous schedules; taking the amount of nitrogen in 1 gm. egg albumen to be ·15 gm. a typical test gave the following figures. In each case the control was tested and figures obtained from control flasks deducted.

Percentage of egg albumen reduced.

	Total	Ammonia	Amino-acids	Peptone
5 days	44·5	4·4	6·0	36·0
10 ,,	51·6	8·1	13·2	30·4
15 ,,	63·9	15·1	2·8	46·0
20 ,,	82·2	15·0	1·2	66·0

The amount of ammonia and peptone increases gradually; the amino-acid, as in the case of the milk flasks, increases and then decreases, the decrease being correlated with an increase in the ammonia content. The large percentage of albumen reduced shows that the organism is a fairly active proteolytic agent.

A fair amount of ammonia is also produced in media containing peptone, *e.g.* ordinary nutrient bouillon.

Broth cultures after sterilisation cause no peptonisation of milk. If a culture is killed by exposing it to a temperature of about 55° C. for half-an-hour, and then 3–5 c.c. of the culture run into each of a number of tubes of litmus milk, there is no change in the milk during ten days. *Bacterium nectarophilum* gave positive results with this test, the milk being slowly cleared in the same way as when the organism was growing in the medium.

Amylolytic action. The starch of steamed potato cylinders is not destroyed at all rapidly; cylinders on which the organisms had been growing for three weeks still gave a strong blue black reaction with iodine.

Tubes containing 10 c.c. nutrient bouillon and ·01 gm. soluble starch were planted with a vigorous culture and incubated at 30° C. It was only after 14 days that the starch entirely disappeared. When a similar set of tubes was planted with *Bacterium citri* the starch had entirely disappeared at the end of 48 hours; the amylolytic action of the tomato organism is therefore comparatively feeble.

Cultures in nutrient broth which had been incubated for five days at 30° C. were tested for the presence of diastase. A mixture was made of equal quantities of the cultivation and a thin starch paste containing 2 per cent. thymol; this was placed in the incubator at 37° C. for six hours and then tested with Fehling's solution, with negative results. Control cultures of *Bacillus subtilis* tested in the same way gave a good reaction for reducing sugars.

Production of invertase. Nutrient bouillon in which the organism had been growing for five days was tested for the presence of invertase. A mixture was prepared containing equal quantities of the cultivation and a 2 per cent. solution of cane sugar to which 2 per cent. of carbolic acid had been added. After several hours the mixture was tested for reducing sugars with negative results.

When the organism is grown in nutrient broth containing cane sugar, however, a certain amount of reducing sugar is produced. In flasks containing 500 c.c. of nutrient broth with 2 per cent. saccharose, the organism produced 61 mg. of reducing sugar in three days, and at the end of five days the culture contained 159 mg. of reducing sugar.

Gas formation. No *gas* was produced in fermentation tubes containing nutrient broth and 2 per cent. of following substances: dextrose, laevulose, saccharose, maltose, lactose, mannite, dextrin, galactose, glycerine. In no case was any growth observed in the closed end of the tube. There was a small amount of alcohol in the distillate from cultures in dextrose bouillon. In tube cultivations in iron and lead peptone solution and broth, there was a slight discolouration of the precipitate after three weeks, showing that traces of sulphuretted hydrogen are liberated.

Acid production. The behaviour of the organism in the various sugar broths very closely resembles that of *Bacterium campestre* and other organisms of this group, that is to say, it produces a small amount of acid from certain sugars but the acid production is very rapidly obscured by the formation of alkali, probably in the form of ammonia, which has shown to be produced in appreciable quantities in peptone broth.

In dextrose bouillon the acidity is more marked than in any of the other media, the greatest acidity being observed about the fifth day; the acidity of the medium gradually decreases and after three or four weeks it becomes neutral or slightly alkaline.

The same may be said of cultures in nutrient bouillon with 2 per cent. laevulose, saccharose, lactose, galactose, glycerine, and dextrin, but less acid is produced with any of these substances than with dextrose. No definite acid formation was observed in flasks containing mannite and maltose.

Indol and phenol production. Cultures in nutrient bouillon and Dunham's solution were repeatedly tested for indol on the third, fifth and tenth day, but with negative results. No reaction was obtained with a nitrite and sulphuric acid, nor with the Rosindol test.

Cultures in nutrient bouillon tested on the tenth day also gave a negative reaction for phenol.

Reducing agent formation: colour destruction. A number of tube cultivations were prepared in nutrient bouillon tinted with litmus, rosolic acid, neutral red, methyl orange, and methylene blue: no colour reduction was observed.

Nitrate reduction. A number of tube cultivations in nitrate bouillon were tested after three, five and ten days. Some of these showed a trace of nitrite but in others no reaction was obtained. The controls gave no reaction for nitrite.

Flasks of nitrate bouillon tested after ten days contained slightly more ammonia than similar flasks containing bouillon without potassium nitrate. These tests were repeated several times with no more decided results; it would seem therefore that the organism has a feeble action on nitrates, and that traces of nitrite and ammonia are at times produced in culture solutions containing a nitrate.

Atmosphere. The organism is strictly aerobic and makes no growth in the depth of media nor in the absence of oxygen. No growth took place in Bulloch's apparatus in an atmosphere of hydrogen, nitrogen or carbon dioxide, but except in the case of tubes exposed to CO_2 the organism was not killed and began to grow when removed from the apparatus and placed in the incubator.

Temperature. This bacterium grows through a wide range of temperature, it grows slowly at 5° C. and at 40° C.; the optimum is about 30° C. It is killed by a prolonged exposure to 42° C. The thermal death point (moist, ten minutes' exposure) is 56° C.; in dry tubes the organism did not grow after ten minutes' exposure to a temperature of 64° C.

Reaction of medium. This bacterium does not grow at all in an alkaline bouillon, even if only − 5 of Fuller's scale; it grows very slowly in bouillon neutral to phenol-phthalein. It grows well in bouillon with a natural reaction of + 25, the optimum being about + 20 of Fuller's scale; it grows almost as well at + 15 as at + 20. A number of cultures were also made in broth which had been made neutral and acidified with various acids. It grew well in + 20 (Fuller), malic, lactic, tartaric, hydrochloric and citric acids; in tubes with a reaction of + 25 Fuller, it grew in tubes acidified with malic, lactic and citric acids and not with tartaric or hydrochloric acids; it is much less sensitive to malic and citric acids, growing unrestrainedly in bouillon with a reaction of + 30 Fuller, and clouding bouillon up to + 50 Fuller, malic acid and + 60 citric acid; the inhibition point for these was + 55 and + 65 respectively.

Toleration of sodium chloride. Growth is inhibited by 4 per cent. of sodium chloride; the organism grows freely in nutrient bouillon containing 3 per cent. sodium chloride.

Resistance to fungicides. Tests were made in nutrient bouillon containing various percentages of copper sulphate, phenol, mercuric chloride and formalin. Tubes were planted fairly heavily and after ten minutes a plate was poured from each dilution. In this way the inhibition coefficient and lethal coefficient were determined.

The organism is killed by ten minutes' exposure to copper sulphate

1 : 25; phenol 1 : 500; mercuric chloride 1 : 500 and formalin 1 : 200. It is extraordinarily resistant to copper sulphate, the lethal coefficient for *Bacillus mangiferae* being about 1 : 400. The inhibition coefficient was not determined very exactly; the bacterium grows in a bouillon containing 1 : 1000 copper sulphate, but was inhibited by 1 : 800; the same result was obtained with formalin. The organism grows in bouillon containing phenol 1 : 800 but not in 1 : 600; similarly it grows in mercuric chloride 1 : 3000 but not in 1 : 2500.

Desiccation. A number of sterile cover slips were covered with a film of the organism and placed in sterile ventilated petri-dishes in a desiccator; one of these was removed each day and dropped into a tube of nutrient bouillon. No growth was obtained from cover slips which had been exposed to desiccation for more than ten days.

NOMENCLATURE.

The name *Bacterium vesicatorium* n. sp. is suggested for this organism, which has apparently not previously been described: its chief characters are as follows:

Bacterium vesicatorium n. sp. A parasite of the tomato plant, causing spots on leaves and stems and raised blisters or cankers in the fruit. A motile rod averaging 1–1·5 × ·6–·7 μ, with rounded ends and a single polar flagellum, occurring singly, in pairs, or in short chains. On nutrient agar colonies appear in 48 hours at 30° C. and are finally circular, about 5 mm. diameter, semi-translucent, Naples yellow in colour. On potato produces a copious yellow, spreading growth, butyrous or rather viscid in consistency. Liquefies gelatine and blood serum; no growth in Uschinsky's and Cohn's solutions: grows slowly but well in Fermi's solution. In milk there is a separation of whey, and casein becomes slowly peptonised. Is a fairly active proteolytic agent, destroys starch very slowly. There is no gas formation in sugar bouillon; there is a slight increase in acidity but bouillon ultimately becomes more alkaline. No definite evidence of nitrate reduction was obtained; no indol or phenol is produced in bouillon or Dunham's solution. The organism is strictly aerobic; grows through a wide range of temperature from 5° C. to 40° C.; the optimum temperature for growth is about 30° C.; thermal death point 56° C. Does not grow in alkaline media, but tolerates a fair amount of acid; growth inhibited by 4 per cent. sodium chloride. Group number 211, 2332523.

Two other yellow organisms have been described as causing diseases of the tomato, *Aplanobacter michiganense* Erw. Sm.(2) and an organism believed to be identical with *Bacillus Lathyri* Manns and Taubenhaus(1).

Aplanobacter michiganense is non-motile, tolerates considerable alkali, growing in − 25 and − 30 peptone bouillon and does not grow in peptone beef bouillon acidified to + 20, + 25, or + 30 with malic or citric acid.

The second organism has four to six peritrichous flagella and grows in Uschinsky's solution: cultures in nitrate broth give a strong reaction for nitrite on the second day.

The three organisms appear to be quite distinct, and *Bacterium vesicatorium* differs considerably from the other two in its effect on the host.

CONTROL OF THE DISEASE.

The organism is not very sensitive to the fungicides usually employed in spraying solutions, and experience has shown that spraying is of little use in combating plant diseases caused by bacteria. This is particularly the case with organisms disseminated chiefly by rain splash and infecting the plant through the stomata.

It appears to be the custom of the market gardeners in the Pretoria district to save seed from their own plants for the following season. This custom is probably in part responsible for carrying over the disease from one season to another. Certain varieties are more susceptible than others, but it has been found practically impossible to discover the name of the varieties usually grown. The following methods are therefore suggested for the control of the disease.

(1) Selection of resistant varieties.

(2) Sterilisation of the seed by means of formalin or mercuric chloride.

(3) A long crop rotation.

(4) Destruction of diseased fruit and of affected plants at the end of the season.

In connection with (3) it will also be of importance that the irrigation furrows shall not be allowed to flow through the old tomato bed to the site selected for tomatoes in the following season.

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EXPLANATION OF PLATE XXVI

Fig. 1. Tomato fruits severely attacked by *Bacterium vesicatorium*.

Fig. 2. A milder form of the canker showing the characteristic blistering in early stages of infection.

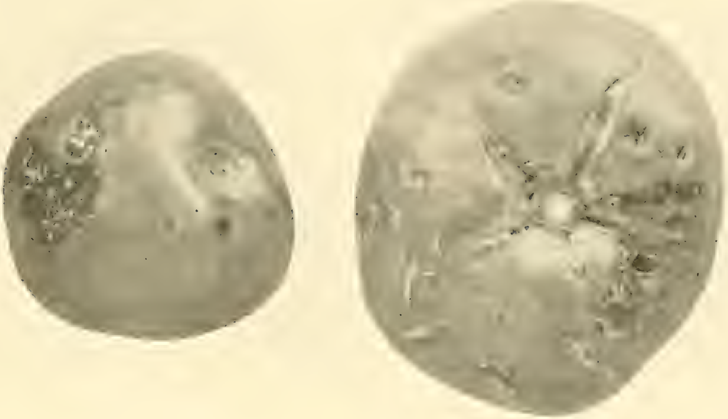

Fig. 1.

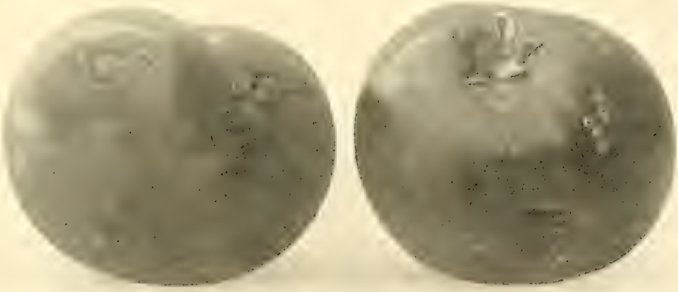

Fig. 2.

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E. E. GREEN, Way's End, Camberley (late Government Entomologist, Ceylon)
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